

# THE POLLEN WASPS

ECOLOGY AND NATURAL HISTORY  
OF THE MASARINAE



SARAH K. GESS



**W**asps of the subfamily Masarinae are sometimes called “pollen wasps” because they are the only wasps that—like bees—provision their nest cells with pollen and nectar. Numbering a little over 300 known species, they favor regions of the world with hot, dry climates and scrubby vegetation, and are especially plentiful and diverse in southern Africa, where Sarah K. Gess has made the study of aculeate Hymenoptera, including these fascinating insects, her life’s work.

The product of more than twenty years of study and field experience, *The Pollen Wasps* is the first new work on masarine wasps since O. W. Richards’s 1962 monograph. It gathers in a single volume current data on all that is known about the masarines: their biogeography, life history, nest-building behavior, myriad flower associations, and associated insects and other microfauna (parasites, scavengers, nest “cuckoos,” and predators). On the basis of her field observations of five plant families and 92 species of pollen wasps, Gess examines the role of these insects as potential pollinators of their forage plants in southern Africa. She also considers trends in land use in this part of the world and evaluates their impact on pollen wasp biodiversity.

The 25 color plates and 60 black-and-white illustrations offer readers a rare close look at this little-known and endangered group of insects. Three appendices list all known flower-visiting records, all hymenopteran visitors to the flowers included in the pollination chapter, and all published species names for Masarinae.

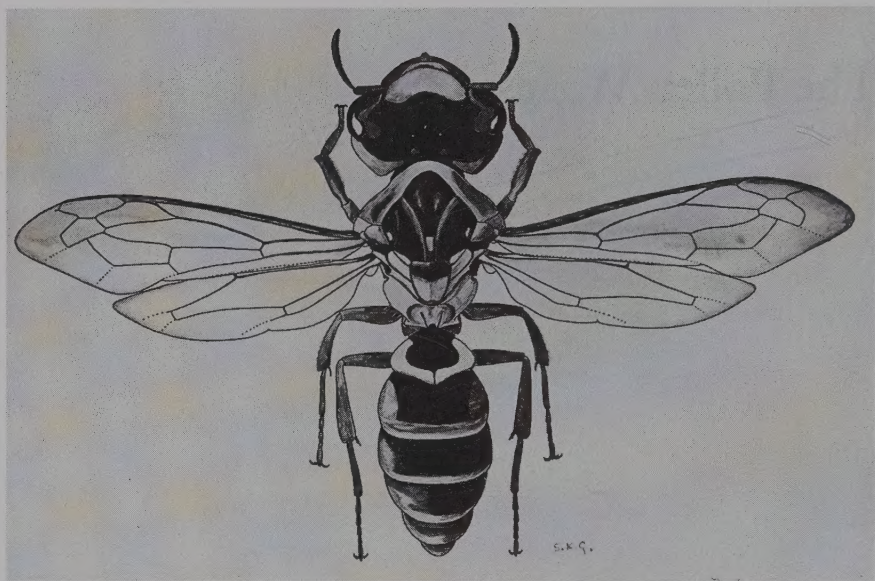
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# The Pollen Wasps



*Ceramius lichtensteinii* (Klug).

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# The Pollen Wasps

*Ecology and Natural History of the Masarinae*

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Sarah K. Gess

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# The Pollen Wasps





# Introduction

The masarine wasps number little over 300 known species, a relatively small group when compared with the 3,000 species of the closely related eumenines. Masarines are the only wasps that provision their nest cells with pollen and nectar, as bees do. It is this behavior which has led to their being called “honey wasps” and “pollen wasps.” These names are not, however, established common names—not like “hornet” and “potter wasp,” which are accepted as part of our language. They should therefore be carefully considered before being popularized by frequent, wide usage. The “honey wasps” (as *Honigwespen*) is German in origin and has been applied to *Celonites abbreviatus*, the only masarine found in the German-speaking European countries. I do not believe that it should be more widely adopted. For one thing, the name is misleading because, as only bees that make honey are known as honeybees, it would be reasonable to assume that wasps called “honey wasps” would make honey too, but masarine wasps do not. Second, the name is ambiguous as it has also been used (Schwarz 1929; Sugden and McAllen 1994) for some of the social wasps that do make honey. The name “pollen wasps” was coined by Houston (1984) and picked up by Carpenter (1993). Its use would not lead to any obvious misconceptions and therefore, for want of a better name, I favor its use.

In the present work I review, synthesize, and discuss what has been learned of the ecology and natural history of the pollen wasps. The only previous attempt to review and discuss the natural history of the pollen wasps (as Masaridae) as a group was that of Richards (1962, pp. 28–34), which appeared at a time when there were few, mostly fragmentary, accounts of nesting and flower visiting. Contributions by Gess and Gess (1980, 1986, 1988a, 1988b, 1989, 1990, 1992) on *Ceramius*, *Jugurtia*,

*Masarina*, *Celonites*, and *Quartinia* in southern Africa, Houston (1984, 1986) and Naumann and Cardale (1987) on *Paragia* and Gess et al. (1995) on *Rolandia* in Australia, and Richards (1963b) and Torchio (1970) on *Pseudomasaris* in North America form the bulk of the present review, synthesis, and discussion.

The only previous attempt to assess a pollen wasp as a potential pollinator was that of Torchio (1974) in his study of *Penstemon* (Scrophulariaceae) and *Pseudomasaris vespoides*. After reviewing the biogeography, flower associations, life history, nesting, and the associates of the pollen wasps, I examine the role of these wasps in southern Africa as potential pollinators of their forage plants through a study of five plant families and 92 species of pollen wasps. This I follow with a brief consideration of the trends in land use in the semi-arid areas of southern Africa and of how these are likely to affect pollen wasp biodiversity.

### *Taxonomic history of the masarine wasps*

The pollen wasps are here treated as a subfamily, the Masarinae. The taxonomic history of this group stems from the description of a family Masarides by Latreille (1802). Latreille's family derived its name from the genus *Masaris* Fabricius, 1793. The first masarine to be described was, however, not a species of *Masaris* but of *Celonites*, *C. abbreviatus*, originally named as a species of *Vespa* by Villers in 1789.

In the interval since 1802 the taxon has been variously delimited and ranked but has always been grouped with the "vespids" and "eumenids" (Latreille 1825; Shuckard 1837; Spinola 1851; Bequaert 1918, 1929; Bradley 1922; Richards 1962; Giordani Soika 1974; Carpenter 1982, 1987, 1988, 1991, 1993, in prep. b). The first standard classification of the Vespoidea is that of Bradley (1922) modified by Bequaert (1928). This was followed by that of Richards (1962), which was based on the examination of a wide range of species, and that of Carpenter (1982), which was based on a cladistic analysis in which he investigated the monophyly and interrelationships of all the suprageneric taxa. (See Table 1.)

Richards's superfamily Vespoidea is constituted of three families, Eumenidae, Vespidae, and Masaridae, and Masaridae is constituted of three subfamilies, Euparagiinae, Gayellinae, and Masarinae. Richards based his discussion of the phylogeny of the Vespoidea on characters which he considered to be most characteristic of the group and least often

Table 1. Three classifications of the Vespoidea.

Bradley (1922) and Bequaert (1928)	Richards (1962)	Carpenter (1982)
VESPIDAE	VESPOIDEA	VESPIDAE
Euparagiinae	Masaridae Euparagiinae	Euparagiinae Masarinae
Gayellinae	Gayellinae	Gayellini
Masaridinae	Masarinae	Masarini
Paragiini	Paragiini (includes Masaridini in part)	
Masaridini	Masarini (includes Masaridini in part)	
Raphiglossinae	Eumenidae	Eumeninae
Zethinae	Raphiglossinae	
Eumeninae	Discoeliinae	
	Eumeninae	
Stenogastrinae	Vespidae	
Vespinae	Stenogastrinae	Stenogastrinae
	Vespinae	Vespinae
	Polistinae	Polistinae
Epiponinae	Polybini	
Polistinae	Polistini	
Ropalidiinae	Ropalidiini	

seen in any other group. He considered that the vespoids are derived from the same stock as that which gave rise to the Scolioidea, of which he considered the Tiphidae to be the least specialized modern representative. He thus considered that any character which is characteristically vespoid and is not found in the scoloids is the sign of a group which has proceeded some way on the vespoid path.

He stated that acroglossal buttons (the sclerotized pads at the tips of the glossa and paraglossae) are known only in the vespoids but are absent in the more primitive masarids, and he therefore believed that they must have been separately evolved or reacquired in the higher masarids.

He considered that short, non-crossing mandibles are primitive and that long mandibles have developed separately in the Eumeninae, Gayellinae, and *Ceramius* and probably in *Raphiglossoides*.

Like Bequaert (1929), Richards believed the emargination of the eyes to be an ancestral character since it is also found in some scolioids. Its loss in many Masarinae he considered to be secondary.

He considered the presence of three submarginal cells in the forewings to be primitive and that the majority of the Masaridae are specialized in the loss of one cell. The long median cell ( $M + Cu_1$ ) he considered to be a vespoid specialization and the short median cell of many masarids probably to be the primitive condition. The folding of the wings is a specialization which has not occurred in the majority of masarids, and he therefore believed that in those genera in which it occurs (*Celonites* and *Quartinia*) it must have been acquired by convergence.

He noted the basal ring on the midfemur to be a primitive vespoid character which has been lost in all the masarids except *Euparagia*.

The fusion of the tergite and sternite of the first gastral segment he considered to be a highly characteristic vespoid feature, but he noted that it seems not to have been evolved at the time that the masarids diverged and is not seen in any scolioids except in a few wingless females.

The retraction of the posterior gastral segments within the second he noted as peculiar in the vespoids but absent in the Masaridae except for the Gayellinae, in which he considered that it was acquired independently from the Eumenidae.

Richards noted that the fusion of the male abdominal sternites 8 and 9, noted by Snodgrass (1941) as characteristic of vespoids, is not fully developed in masarids and that more of the 8th sternite is exposed than usual.

Finally, he noted that spine-like parameres are highly characteristic of the vespoids but have been lost in most Masaridae, being, however, retained in the Gayellinae and in a modified form in his Paragiini and in the Euparagiinae.

Richards summarized his speculations on the phylogeny of the Masaridae diagrammatically (Fig. 1). The family was considered by him to be an ancient group which has suffered much extinction. He considered that the most primitive (i.e., the form that most resembles a likely universal ancestor) living masarid is *Euparagia*, the only one that is still predatory (all others provision with pollen and nectar). He considered the Gayellinae to be in some ways (mandibles, clypeus, wing venation, gaster especially of *Paramasaris*, male genitalia) more eumenid-like than any other masarid but doubted that this is due to direct relationship. He considered *Ceramiopsis* to be the nearest thing to a connecting link between the



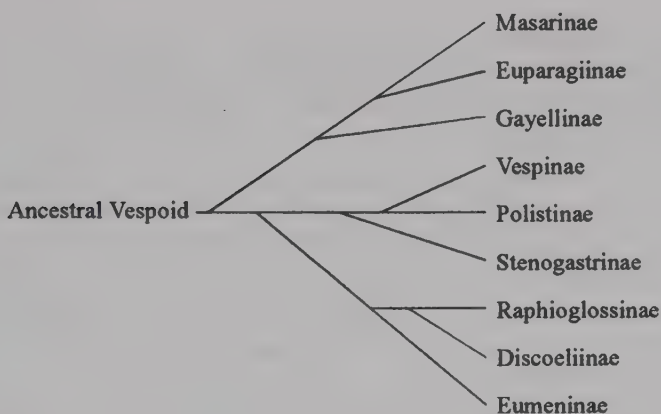


Figure 1. Phylogeny of the subfamilies of the Vespoidea (*sensu* Richards) (from Richards 1962).

*Paragia*-group and the *Ceramius*-group and that *Trimeria* is in several respects a link between his Paragiini and his Masarini.

Carpenter (1982) stated that it is apparent that Richards in his discussion of the phylogeny of the Vespoidea did not distinguish between ancestral and derived states in many critical characters—in other words, that his phylogeny is based upon unanalyzed similarity. Like Charnley (1973), Spradbery (1975), and van der Vecht (1977), Carpenter questioned whether or not Richards's classification is a natural one. In the course of his study Carpenter examined the external morphology of 136 genera and 506 species of Vespoidea, representing all the recognized suprageneric taxa, and 21 genera and 45 species of Scoliidae, representing the two subfamilies and three tribes. He included examples of Scoliidae as the suggested closest relative of the Vespidae following Richards (1962) and Brothers (1975). Characters of the larvae, internal morphology, and behavior were extracted from the literature. The behavioral characters for Masaridae available to him were very limited, as the work of Gess and Gess (1980, 1986, 1988a, 1988b, 1989, 1992), Houston (1984, 1986), Naumann and Cardale (1987), and Gess et al. (1995) had not been noted or not yet been published. Analysis of the data followed the principles of phylogenetic reasoning elaborated by Hennig (1966). The subfamilies and tribes were surveyed for unique features (autapomorphies) to establish their monophyly; these groups were linked by shared features (treated as synapomorphies at this level of analysis) and the most parsimonious

cladogram constructed, that is, one which minimized convergences. Polarities for the characters were then assigned, on the basis of comparison with states found in the sister group of the Vespoidea, the Scoliidae, as well as in other Aculeata. The construction of the most parsimonious cladogram was then repeated, with uninformative characters identified and eliminated. The polarity of these characters was subsequently re-assigned according to their position in the cladogram, in such a way as to minimize homoplasy. The results were checked by computer analyses using Wagner and character-compatibility methods. The result of this thorough investigation is presented in Figure 2.

Carpenter found the outstanding autapomorphies of his Vespidae (Vespoidea in Richards's taxonomy) to be the elongate discal cell (at least the equal of the submedian cell), spined parameres, and oviposition into an empty cell. The sister-group relationship between *Euparagia* and the

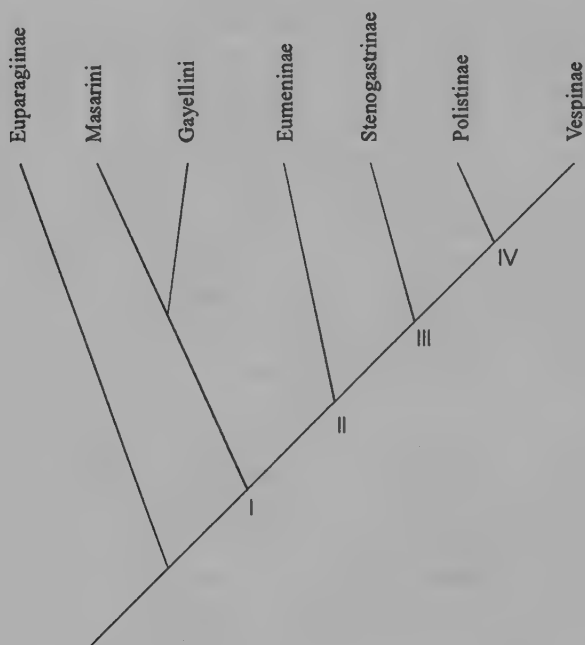


Figure 2. Cladogram of the subfamilies and tribes of the Vespidae (*sensu* Carpenter) (from Carpenter 1982). Roman numerals refer to components listed in Carpenter's section on ground-plan character states.

rest of his Vespidae was established especially by the forewing with the cubito-anal crossvein (cu-a) straight and the hindwing with the anal lobe reduced in all vespids aside from *Euparagia*. Presence of acroglossal buttons also supports this relationship, but these were considered to be secondarily lost in the stenogastrines. Carpenter's Masarini and Gayellini were grouped on the basis of hypostomal apodemes (elongate projections into the oral fossa below the level of the hypostoma and set off from it by a furrow) (lost in some Masarini), loss of the mesoscutal lamella (a raised carina opposite the tegula and produced from the posterolateral corner of the mesoscutum), loss of the midfemural basal ring, and mellifery. Both these groups show independent development of several of the characters that link component II. The hypothesis of a sister-group relationship between them was considered by Carpenter to best describe the distribution of characters.

Based on his analysis Carpenter proposed the classification of the Vespoidea presented in Table 1. Thus in his classification he recognized a single family Vespidae with six subfamilies: Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Polistinae, and Vespinae. He disassociated the Euparagiinae, which provision their nest cells with beetle larvae, from Richards's Gayellinae and Masarinae, which provision with pollen and nectar. At the same time he associated more closely the Gayellinae (*sensu* Giordani Soika 1974) and the Masarinae (*sensu* Richards 1962) by placing them together as tribes (Gayellini and Masarini) in his subfamily Masarinae. This proposal is followed in the present work.

Carpenter and Rasnitsyn (1990) added a seventh, though extinct, subfamily to Carpenter's Vespidae. This subfamily, the Priorvespinae, is placed by them as a sister group of all other Vespidae (*sensu* Carpenter 1982) on the basis of a cladistic analysis using the informative data for vespid families and tribes coded from Carpenter (1982) and Hennig86 (Farris 1988). The result of this analysis is presented in Figure 3. The Euparagiinae are seen as a sister group to the ancestor of all the other extant vespids. Carpenter's Masarinae are seen to be on a line diverging from that giving rise to his Eumeninae, Stenogastrinae, Polistinae, and Vespinae. Thus the line giving rise to the pollen and nectar provisioning masarines in the Vespidae (or Vespoidea) is seen by Carpenter and Rasnitsyn to have been a relatively early divergence in the history of the otherwise predatory Vespidae (or Vespoidea), just as the pollen and nectar provisioning Apidae are seen by Michener (1974) and Brothers

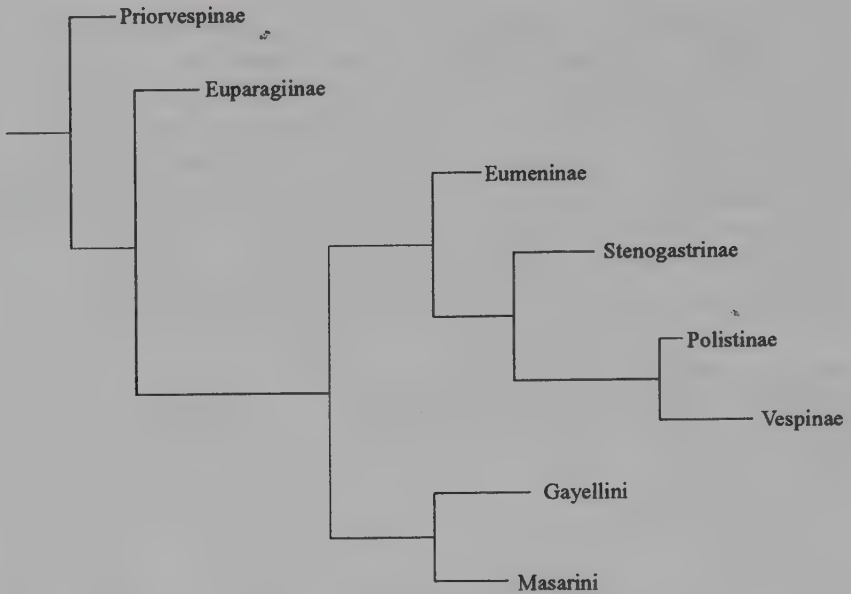


Figure 3. Cladogram of the subfamilies of the family Vespidae (*sensu* Carpenter and Rasnitsyn) and tribes of the subfamily Masarinae (*sensu* Carpenter and Rasnitsyn) (from Carpenter and Rasnitsyn 1990).

(1975) to have been a relatively early divergence in the history of the otherwise predatory Sphecoidea. It should be noted that whereas the most highly eusocial sphecoids, the honeybees, head the line of pollen and nectar provisioners in the Sphecoidea, the pollen and nectar provisioning line in the Vespoidea (the Masarinae) has not led to sociality. (The vespoid wasps commonly known as the “social wasps” head the main vespoid line.)

Within his subfamily Masarinae Richards recognized two tribes, the Paragiini and the Masarini, but the delimitation of these subgroups has been disputed. Richards (1962) considered his Paragiini to be constituted of two subgroups, one including *Paragia* Shuckard, *Metaparagia* Meade-Waldo, *Rolandia* Richards, and *Riekia* Richards, and the other including *Ceramiopsis* Zavattari and *Ceramius* Latreille. Carpenter (1982) concluded that Richards’s Paragiini is paraphyletic and hence did not recognize this grouping. Carpenter (1993), however, has demonstrated by means of a cladistic analysis of the first of Richards’s subgroups within his Paragiini

(the Australian masarines) that this subgroup comprises a monophyletic group, the sister group of Richards's second subgroup of Paragiini together with Richards's Masarini. Carpenter's findings are reflected in the classification followed here (Table 2). By means of a further cladistic analysis Carpenter (1993) analyzed relatedness of genera within the Masarinae as a whole and proposed a cladogram (Fig. 4) resulting from this analysis.

Seven of the 19 genera recognized by Richards (1962) and a genus newly erected by Snelling (1986) are listed by van der Vecht and Carpenter (1990) as junior synonyms:

*Paragayella* Giordani Soika, 1974, as a junior subjective synonym of *Paramasaris* Cameron, 1901

*Riekia* Richards, 1962, *Rolandia* Richards, 1962, and *Ammoparagia* Snelling, 1986, as junior subjective synonyms of *Metaparagia* Meade-Waldo, 1911

Table 2. The subfamily Masarinae as classified for the present work.

Tribe	Subtribe	Genus
Gayellini		<i>Gayella</i> Spinola
		<i>Paramasaris</i> Cameron
Masarini	Paragiina	<i>Paragia</i> Shuckard
		<i>Metaparagia</i> Meade-Waldo
		<i>Riekia</i> Richards
		<i>Rolandia</i> Richards
		<i>Ammoparagia</i> Snelling
	Masarina	<i>Ceramius</i> Latreille
		<i>Ceramiopsis</i> Zavattari
		<i>Trimeria</i> Saussure
		<i>Microtrimeria</i> Bequaert
		<i>Masaris</i> Fabricius
		<i>Pseudomasaris</i> Ashmead
		<i>Jugurtia</i> Saussure
		<i>Masarina</i> Richards
		<i>Celonites</i> Latreille
		<i>Quartinia</i> Ed. André
		<i>Quartinioides</i> Richards
		<i>Quartiniella</i> Schulthess



*Microtrimeria* Bequaert, 1928, as a junior subjective synonym of *Trimeria* Saussure, 1854

*Masarina* Richards, 1962, as a junior subjective synonym of *Jugurtia* Saussure, 1854

*Quartiniella* Schulthess, 1929, and *Quartinioides* Richards, 1962, as junior subjective synonyms of *Quartinia* Ed. André, 1884.

The rationale for the synonymy of *Paragayella* as a junior synonym of *Paramasaris* has been published (Carpenter 1989) and is accepted here. The rationale for the other synonymies has not yet been published, and all the genera involved are retained in the presently used classification (Table 2) and the species list (Appendix 3).

Brothers and Carpenter (1993) gave strong evidence based on cladistic analysis for the broadening of Vespoidea to include 10 families, that is, to combine the families placed by Krombein et al. (1979) in Scolioidea, Formicoidea, Vespoidea, and Pompiloidea. Although this suggestion was adopted in Goulet and Huber (1993), Brothers and Carpenter themselves see a need for further analysis. Therefore, though sympathetic to the proposal, I am for the present adhering to the delimitation of Vespoidea of Carpenter (1982).

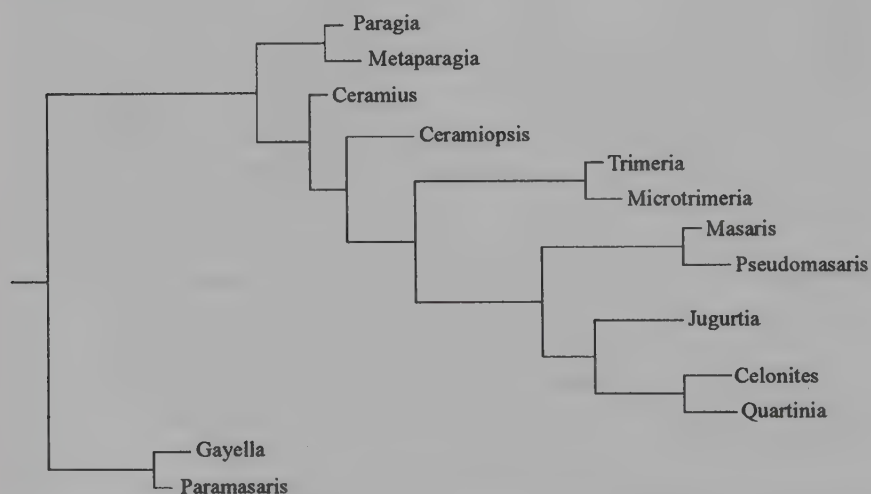


Figure 4. Cladogram of the genera of the subfamily Masarinae (*sensu* Carpenter) (from Carpenter 1993).

*A note on terms used*

In the present study I depart from the use, as in my earlier publications, of old plant family names, such as Compositae, Umbelliferae, and Labiatae, and adopt the presently preferred names following Cronquist (1988). The previously used names are given in parentheses to avoid confusion. The family Aizoaceae has been variously delimited. In the present account I have followed the assessment of Bittrich and Hartmann (1988). Following Hartmann (1991), I use the collective term Mesembryanthema for all Aizoaceae which have petaloid staminodes, in fact for those plants commonly termed "mesems."

I have used one *r* in the spelling of the biome in southern Africa called "Karoo" and *rr* in the spelling of the adjective "karroid." This follows current usage (Acocks 1975; Huntley, 1989; and the ongoing publications of the Karoo Biome Project of the National Programme for Ecosystems Research).

The positions of eight study areas in southern Africa repeatedly referred to in the text are shown in Figure 8.

# Biogeography

The biogeography of the pollen wasps presented here is largely based on my 1992 account (Gess, 1992a) and is confined to present distributions. Carpenter (1982) stated that masarines are Gondwanan in origin, a statement which he later supported by cladistic analysis (Carpenter 1993).

### *World distribution, diversity, and areas of endemism*

Certain generalizations can be made concerning the world distribution of the Masarinae as deduced from published records (Bequaert 1928, 1929, 1940, 1943; Blüthgen 1958, 1961a, 1961b; Blüthgen and Gusenleitner 1970; Blüthgen and Königsmann 1969; Fischer 1964; Fritz 1968; Gess 1965, 1968, 1973, 1989, 1992, 1995; Gess and Gess 1980, 1986, 1988a, 1988b, 1989, 1990, 1992; Giordani Soika 1957, 1961, 1974; Gusenleitner 1966, 1973, 1977, 1988, 1990a, 1990b, 1991, 1992a, 1992b, 1994; Houston 1984, 1986; Menke 1990, 1993; Naumann and Cardale 1987; Neff and Simpson 1985; Panfilov 1961, 1968; Parker 1967; Perez 1989; Richards 1962, 1963a, 1963b, 1964, 1966, 1968, 1969, 1982, 1985; Rossi 1790; Schwarz 1994; Snelling 1986; Wharton 1980; Willink 1963; Willink and Ajmat de Toledo 1979; and Zucchi et al. 1976) (Fig. 5). Masarines have not been found to occur further north than 50°N or further south than 50°S. Within these limits they have, furthermore, not been recorded from eastern North America or from eastern and southern Asia. Records are concentrated in Mediterranean and temperate to hot, semi-arid to arid areas outside the tropics as delimited by di Castri et al. (1981), Evanari et al. (1985, 1986), and West (1983) (Fig. 6). Concerning these areas, Schmida (1985) has stated that they exhibit a north-to-south (or south-to-north, as



Figure 5. The world distribution of the Masarinae (based on published records).



Figure 6. The distributions of the Mediterranean (*black*) and the temperate to hot, semi-arid to arid (*grey*) areas of the world, as defined in di Castri, Goodall, and Specht (1981), Evanari et al. (1985, 1986), and West (1983).

Table 3. Representation in zoogeographical regions of the taxa of Masarinae.

Zoogeographical region	Tribe	Subtribe	Genus
Nearctic	Gayellini		None
	Masarini	Paragiina	None
		Masarina	<i>Pseudomasaris</i> Ashmead
Neotropical	Gayellini		<i>Gayella</i> Spinola
			<i>Paramasaris</i> Cameron
	Masarini	Paragiina	None
		Masarina	<i>Trimeria</i> Saussure
			<i>Microtrimeria</i> Bequaert
			<i>Ceramiopsis</i> Zavattari
Palaearctic	Gayellini		None
	Masarini	Paragiina	None
		Masarina	<i>Ceramius</i> Latreille
			<i>Quartinia</i> Ed. André
			<i>Celonites</i> Latreille
			<i>Jugurtia</i> Saussure
			<i>Masaris</i> Fabricius
Afrotropical	Gayellini		None
	Masarini	Paragiina	None
		Masarina	<i>Ceramius</i> Latreille
			<i>Quartinia</i> Ed. André
			<i>Quartinioides</i> Richards
			<i>Quartiniella</i> Schulthess
			<i>Celonites</i> Latreille
			<i>Jugurtia</i> Saussure
			<i>Masarina</i> Richards
Australian	Gayellini		None
	Masarini	Paragiina	<i>Paragia</i> Shuckard
			<i>Metaparagia</i> Meade-Waldo
			<i>Riekia</i> Richards
			<i>Rolandia</i> Richards
			<i>Ammoparagia</i> Snelling
		Masarina	None



in Argentina; Mares et al. 1985) or west-to-east macrogradient in which the winter rains diminish and the summer rains increase. Between such areas there is a broad similarity in the progression of vegetation types along the macrogradient from Mediterranean climates to extreme deserts—from a dense maquis on the mesic side of the gradient, the vegetation becomes progressively more open, low, and sparse. The level of shared plant families is high but that of shared genera is low.

The representation in zoogeographical regions of the taxa is presented in Table 3. The tribe Gayellini is restricted to the Neotropical Region whereas the tribe Masarini is more widespread, being represented in the Nearctic, Neotropical, Palaearctic, Afrotropical, and Australian regions. Within the Masarini the subtribe Paragiina is endemic to the Australian Region. The subtribe Masarina, on the other hand, is absent from the Australian Region but is represented in the Palaearctic, Afrotropical, Neotropical, and Nearctic regions. At the generic level, the Masarina of the Nearctic and Neotropical regions are distinct from each other, and from those of the Palaearctic and Afrotropical regions combined. Four genera are common to the Palaearctic Region and to southern Africa within the Afrotropical Region, but there are no shared species. A fifth genus is endemic to the Palaearctic and three further genera are endemic to southern Africa within the Afrotropical Region.

One species, *Quartinia indica*, has been recorded from the Oriental Region. This record is for Deesa (22.04N, 36.23E), India. As at least 50 species of *Quartinia* (*sensu stricto*) have been recognized from the Palaearctic and Afrotropical regions, and as Deesa is close to the accepted boundary between the Palaearctic and the Oriental regions, masarines cannot really be considered to have an Oriental distribution. This is in keeping with the statement in Roubik (1989) that the bee species of the northern and xeric areas of India are Palaearctic rather than Oriental species. It is also supported by a consideration of the phytogeography of the area, the proportion of Indo-Malayan flora to Perso-Arabian flora being 1:7 (Gupta 1986).

### *Southern African distribution, areas of diversity, and degree of endemism*

The distribution of pollen wasps in southern Africa plotted as number of species per degree square is shown in Figure 7. If this distribution is compared with that of Mediterranean and semi-arid areas in southern

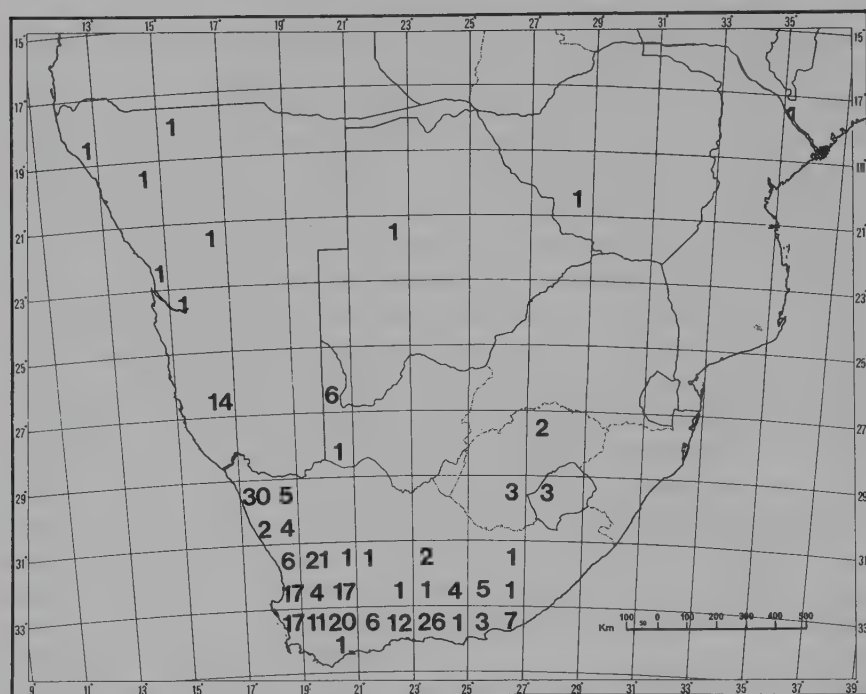


Figure 7. The distribution of Masarinae in southern Africa plotted as number of species per degree square.

Africa—the Fynbos, the Succulent Karoo, and Nama Karoo biomes of Rutherford and Westfall (1986) (Fig. 8)—it is clear that the pollen wasps of southern Africa are largely confined to these biomes. Furthermore, the nodes of greatest diversity are located in the western and southern Karoo and in the southwest at the interface between the Karoo and the Fynbos.

The Fynbos Biome encompasses a broad category of evergreen sclerophyllous heathlands and shrublands in which fine-leaved low shrubs and rush-like plants (Restionaceae) predominate (Hilton-Taylor and le Roux 1989) (Plate 5). It includes five of the Veld Types of Acocks (1953, 1975). An acceptable definition for and classification of fynbos is still a matter of debate, however, and relevant phytosociological studies have been and are being pursued (Cowling and Holmes 1992). The number of masarine species apparently associated with the Fynbos is somewhat skewed. The degree square 33S, 23E, with a count of 26 species, would, from a com-

parison with Figure 8, appear to be in an area of fynbos. Although fynbos vegetation does indeed occur on the high-lying ground, the vegetation of the low-lying ground is karroid with a strong succulent element and it is with this vegetation that the 26 masarine species are associated. Similarly, in the extreme west there is in Figure 8 an oversimplification. Degree square 32S, 18E, with a count of 17 masarine species, appears to be in an area of fynbos whereas it is in fact a mosaic of fynbos and karroid scrub. In this instance the 17 masarine species are associated with vegetation made up of dry fynbos species with an admixture of succulent karoo species.

The Succulent Karoo and the Nama Karoo, collectively known as the Karoo, can be divided into three climatic regions characterized by (1) predominantly winter rainfall; (2) predominantly spring and autumn



Figure 8. The distributions of the Fynbos (*dark grey*), the Succulent Karoo (*medium grey*), the Nama Karoo (*light grey*), and the Desert (*pale grey*) biomes, after Rutherford and Westfall (1986). Positions of a selection of masarine habitats are indicated as follows: K = Lower reaches of the Nossob River Valley, Kalahari Gemsbok National Park; G = Goegab Nature Reserve, Springbok; N = Nieuwoudtville; CW = Clanwilliam; C = Ceres; T = Tierberg; O = Onverwacht; H = Hilton. (See also Plates 1–8.)

rainfall; and (3) predominantly late summer rainfall. Plant growth and flowering and insect activity are seasonal and linked to the rainfall pattern. The mean annual rainfall varies from less than 100 mm to 500 mm but is rarely more than 250 mm. Cyclical droughts are a feature of the spring and autumn—and of the summer-rainfall areas. Rainfall decreases over six-to-ten-year periods and increases over alternating six-to-ten-year periods, the length of the periods varying spacially and temporally (Novellie 1988). There are large temperature fluctuations, both daily and seasonal.

The western Karoo, lying in the winter-rainfall region, is characterized by a noticeable succulent element and is consequently known as the Succulent Karoo (Fig. 8 and Plate 2). It is constituted of seven of Acocks's Veld Types. The central and eastern Karoo, lying in the late-summer-rainfall region and having a markedly lower succulent element, are together known as the Nama Karoo (Fig. 8). This is constituted of 21 of Acocks's Veld Types. The southern (Plate 6) and southeastern Karoo (Plate 8) and the Little Karoo (Plate 7), with a predominantly spring and autumn rainfall, show a progressive decrease in the succulent element from west to east. The vegetation of the Karoo as a whole is characterized by dwarf open shrubland dominated by Asteraceae and Aizoaceae.

The vegetation of the Succulent Karoo (Hilton-Taylor and le Roux 1989) is low to dwarf (usually 1 m tall), open to sparse (15 to 50 percent canopy cover) succulent shrubland. This shrubland is dominated by stem and leaf succulents (particularly of the families Aizoaceae, Crassulaceae, Asclepiadaceae, and Euphorbiaceae), fine-leaved evergreen shrubs, and some obligatory deciduous shrubs. Grasses are infrequent and mainly annuals. The mass flowering displays of annuals (mainly Asteraceae) and geophytes (Liliaceae *sensu lato* and Iridaceae) in spring, particularly in disturbed areas, are characteristic. Low trees are common on rocky outcrops and along river courses. The diversity of the succulent species is unparalleled elsewhere in the world. This, together with the geophytic and annual taxa, makes the Succulent Karoo a unique biome of international importance.

The vegetation of the Nama Karoo (Hilton-Taylor and le Roux 1989) is low to dwarf, open to sparse (see previous definitions), grassy shrubland. The shrubland is dominated by facultatively deciduous shrubs, some leaf succulents, and perennial grasses. Grasses become more dominant from

west to east. Scattered trees grow on rocky outcrops, low hills, and along river courses. The Nama Karoo does not appear to have a species-rich or unique flora. Many of the plant species are shared with the Savannah, Grassland, Succulent Karoo, and Fynbos biomes.

*Ceramius*, *Jugurtia*, *Celonites*, and the *Quartinia* group have distributions (Fig. 9a–d) similar to that of the pollen wasps as a whole. The distribution of *Masarina* appears to be somewhat more limited, being apparently confined to the Fynbos and Succulent Karoo (Fig. 9e).

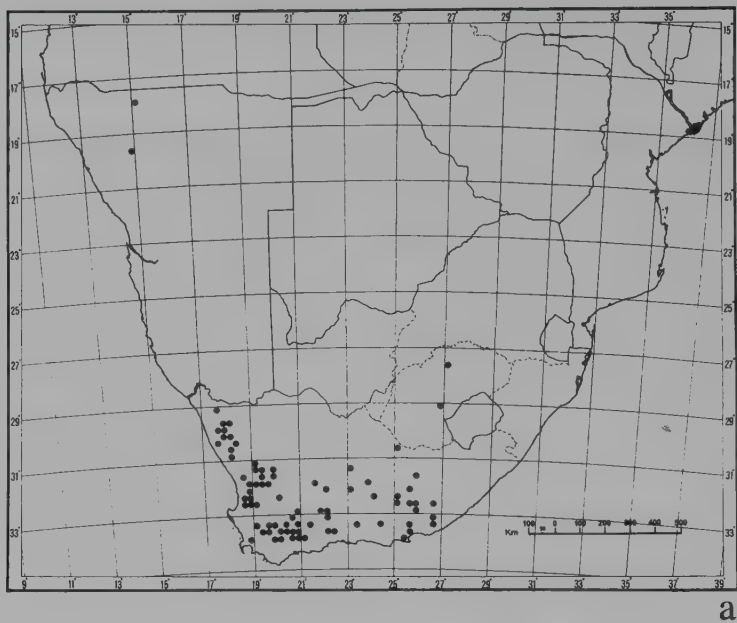
In southern Africa *Ceramius* is the only genus for which the taxonomy and behavior are sufficiently well known that a more detailed consideration of species distributions is warranted. The genus *Ceramius* has been divided on morphological characters into eight species groups (Richards 1962, amended by Gess and Gess 1986, 1988b, 1990) (Table 4). These groupings are supported by nest structure and forage plant associations (Gess and Gess 1986, 1988b, 1990, and unpublished fieldnotes).

With the exception of groups 1 and 7, which are endemic to the Palearctic, all of these species groups are endemic to southern Africa.

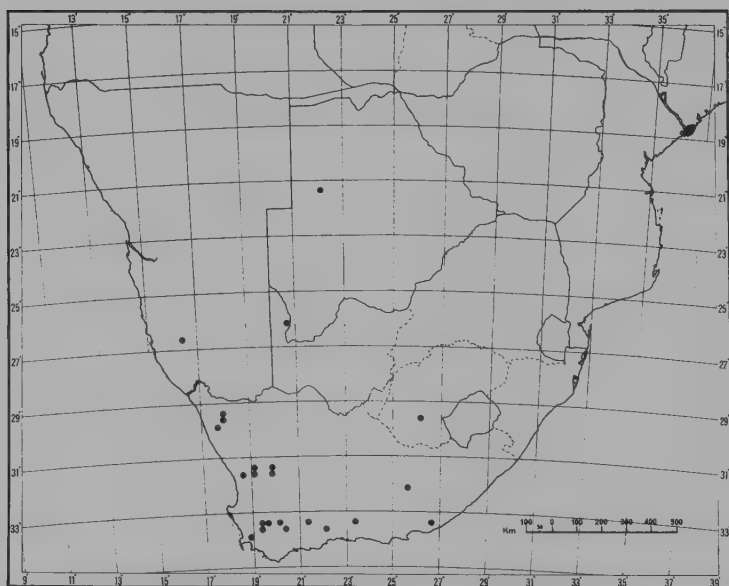
Table 4. Species groups of *Ceramius* (Richards 1962, amended by Gess and Gess 1986, 1988, and 1990).

Species group	<i>Ceramius</i> species included in group
Group 1	<i>fonscolombei</i> Latreille, <i>caucasicus</i> Ed. André, <i>buresschi</i> Atanassov
Group 2 A	<i>cerceriformis</i> Saussure, <i>peringueyi</i> Brauns
Group 2 B	<i>chypeatus</i> Richards, <i>richardsi</i> Gess
Group uncertain	<i>micheneri</i> Gess
Group 3	<i>nigripennis</i> Saussure, <i>toriger</i> Schulthess, <i>braunsi</i> Turner, <i>jacoti</i> Richards
Group 4	<i>beyeri</i> Brauns and probably <i>damarinus</i> Turner
Group 5	<i>lichtensteinii</i> (Klug)
Group 6	<i>caffer</i> Saussure, <i>metanotalis</i> Richards, <i>rex</i> Saussure
Group 7	<i>hispanicus</i> Mercet, <i>moroccanus</i> (G. Soika), <i>spiricornis</i> Saussure, <i>beaumonti</i> (G. Soika), <i>lusitanicus</i> Klug, <i>tuberculifer</i> Saussure, <i>bischoffi</i> Richards
Group 8	<i>bicolor</i> (Thunberg), <i>linearis</i> Klug, <i>capicola</i> Brauns, <i>socius</i> Turner



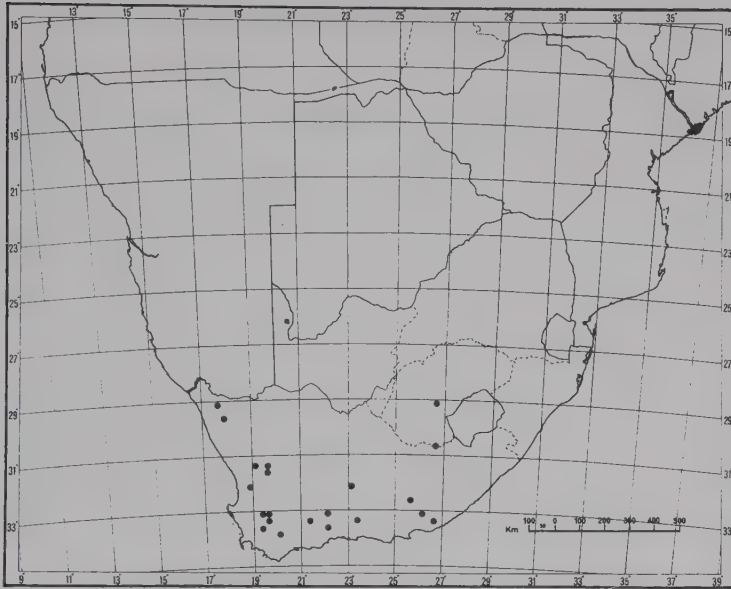


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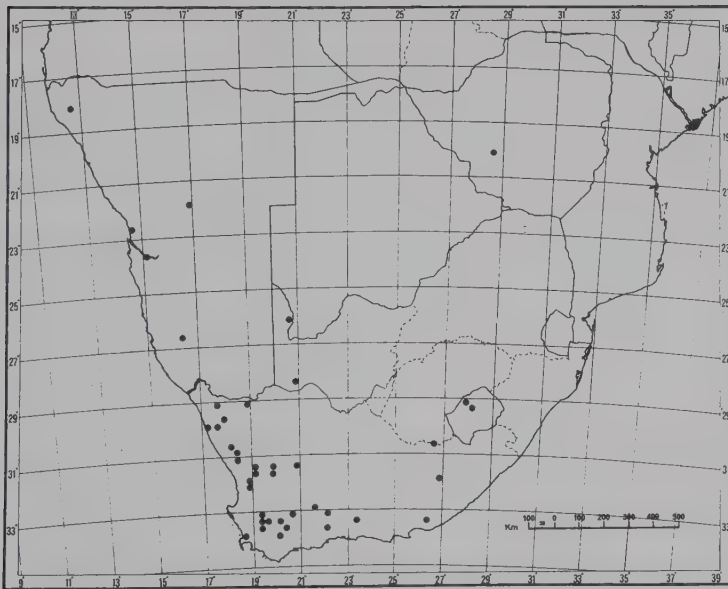


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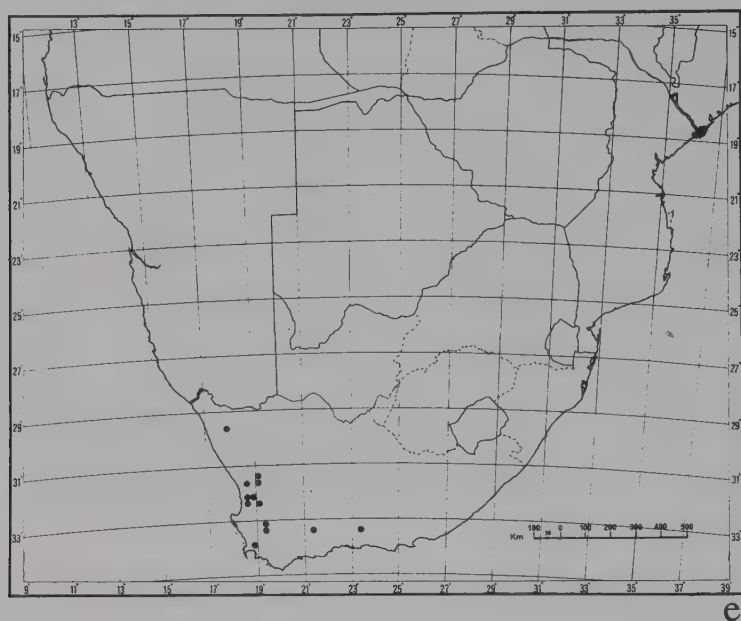
Figure 9. The distributions of the southern African masarine genera: (a) *Ceramius*; (b) *Jugurtia*; (c) *Celonites*; (d) the *Quartinia* group (*Quartinia*, *Quartinioides*, and *Quartiniella*); (e) *Masarina*.



c



d

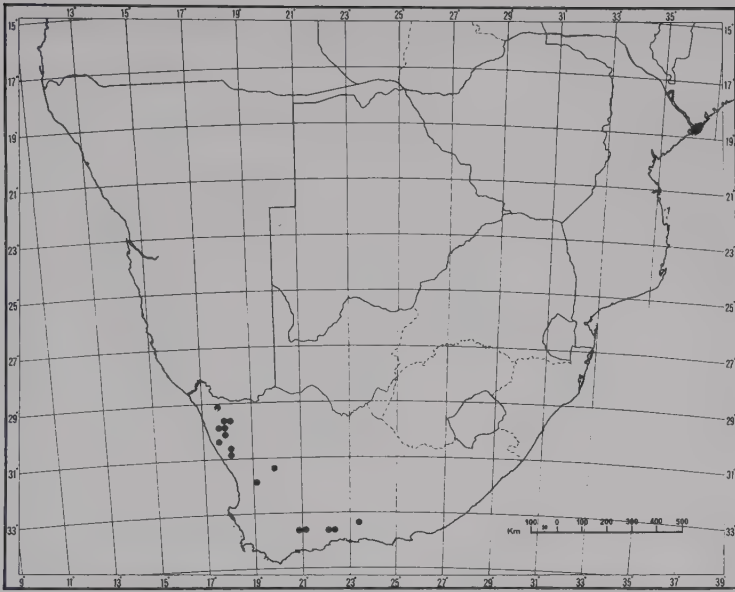


Groups 5 and 8, all species of which forage on *Mesembryanthema* (Aizoaceae), are distributed throughout the greater part of the distribution range of the pollen wasps as a whole (Figs 15. and 17).

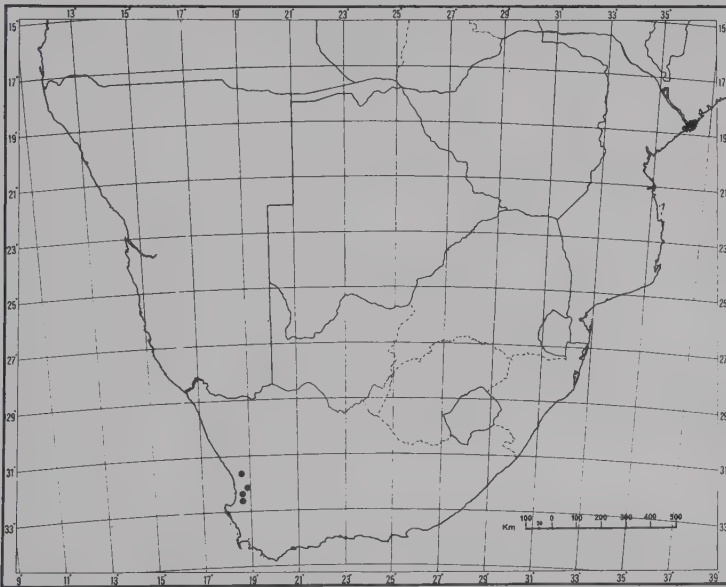
Group 4 has a surprisingly disjunct distribution: *C. beyeri*, which forages on *Mesembryanthema*, has a relatively wide southern distribution (Fig. 14a), and *C. damarinus*, for which forage plants have not been recorded, is restricted to northern Namibia (Fig. 14b).

Group 2A, both species of which forage on *Mesembryanthema*, has a western and southern distribution. *C. cerceriformis* is found throughout the group's distribution range (Fig. 10a), and *C. peringueyi* seems to be the most restricted of the species foraging on *Mesembryanthema*, having been recorded solely from southern Namaqualand to north of the Olifants River Mountains (Fig. 10b).

Groups 3 and 6, all species of which forage on Asteraceae, are relatively limited in distribution, Group 3 being restricted to the western and southwestern Cape (Fig. 13) and Group 6 to the extreme western Cape (Fig. 16). The individual species in Group 3 show very little overlap in their distributions. Those of Group 6 are completely discrete and very restricted: *C. caffer* is distributed to the south of the Olifants River Moun-

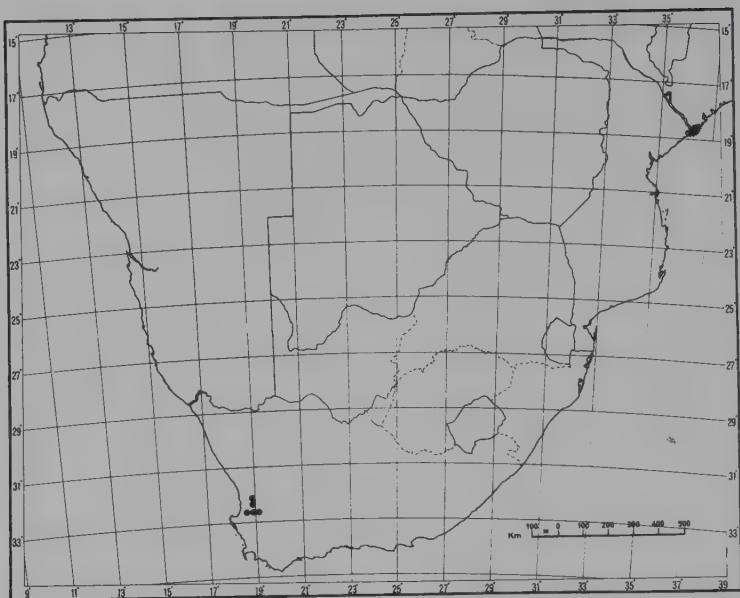


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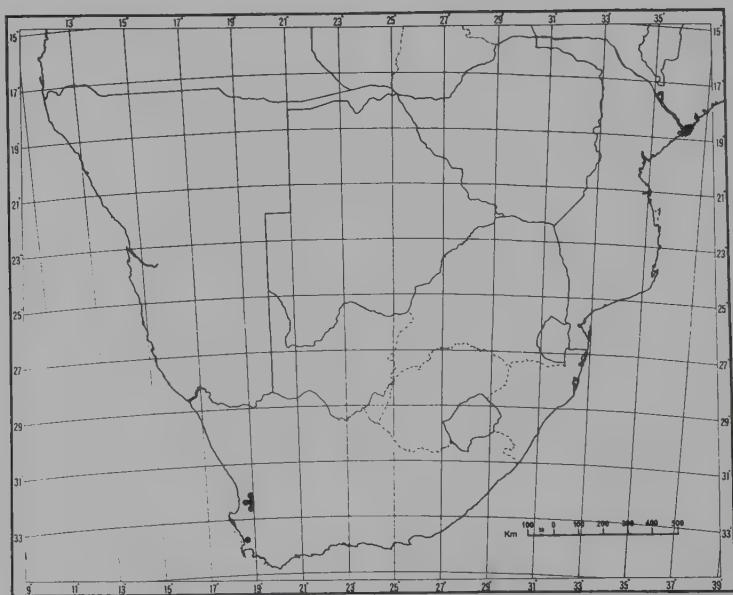


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Figure 10. The distributions of the species of *Ceramius* Group 2A: (a) *Ceramius cerceriformis*; (b) *Ceramius peringueyi*. Both species forage on *Mesembryanthema* (Aizoaceae).



a



b

Figure 11. The distributions of the species of *Ceramius* Group 2B: (a) *Ceramius clypeatus*, which forages on *Aspalathus* (Papilionaceae); (b) *Ceramius richardsi*, which forages on *Aspalathus* (Papilionaceae).



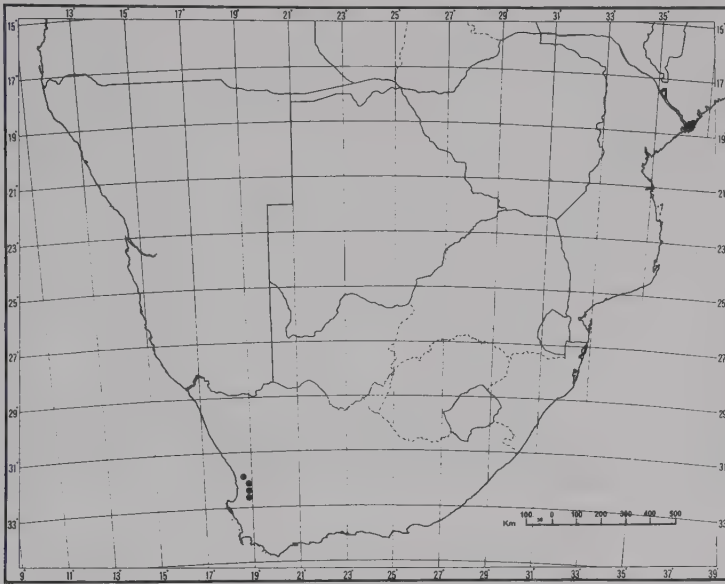
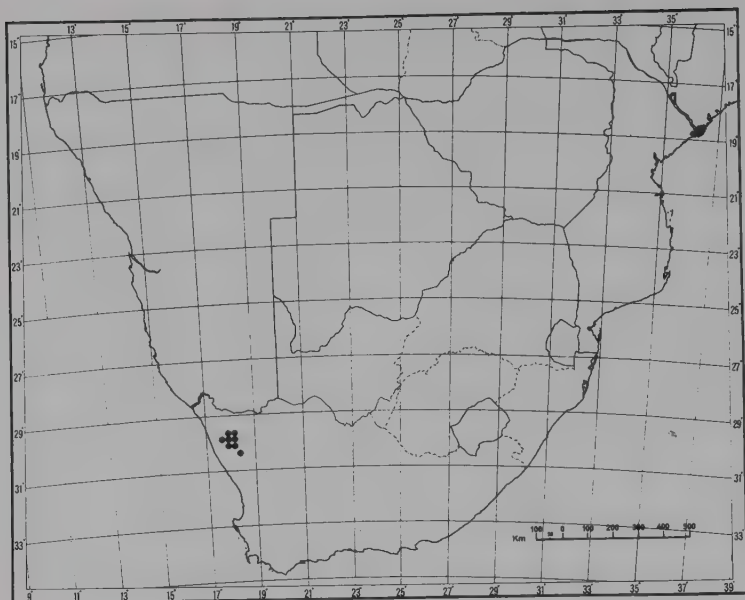


Figure 12. The distribution of *Ceramius micheneri* (Group uncertain, morphologically closest to Group 2B), which forages on *Aspalathus* (Papilionaceae).

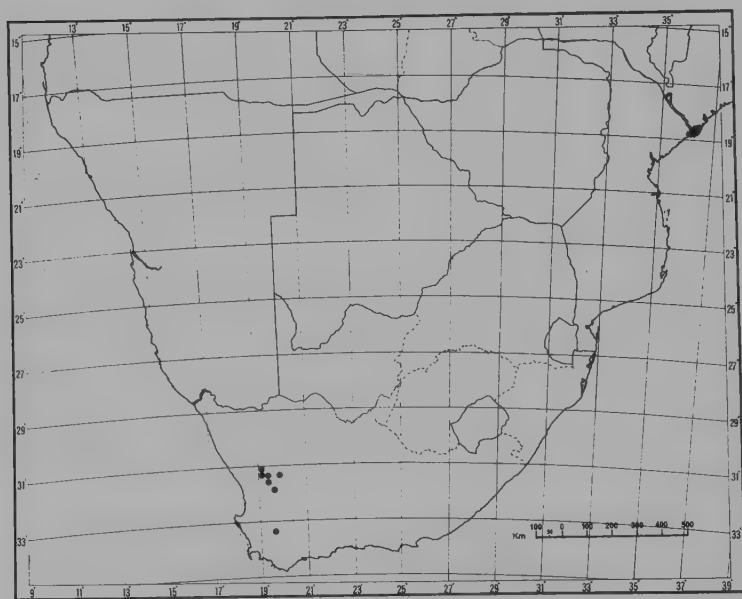
tains (Fig. 16a); *C. metanotalis* to the north of these mountains but to the south of Namaqualand (Fig. 16b); and *C. rex* in the area of Namaqualand termed Klipkoppe (Fig. 16c).

The two species of Group 2B, *C. richardsi* and *C. clypeatus*, and *C. micheneri* forage on Papilionaceae. *C. clypeatus* and *C. micheneri* seem to be restricted to *Aspalathus* and to a small area in and adjacent to the southern Olifants River Valley to the north of the Olifants River Mountains (Figs. 11a and 12). *C. richardsi* has been recorded not only from the southern Olifants River Valley but also from south of the Olifants River Mountains (Fig. 11b).

From this survey of the distributions of the *Ceramius* species it can be concluded that although all the species of southern African *Ceramius* are relatively narrowly endemic, most of the species associated with the Mesembryanthema group of the Aizoaceae are more widely distributed than those species associated with Asteraceae and Papilionaceae. Among the latter, furthermore, there are species which can be considered to be extremely narrowly endemic.

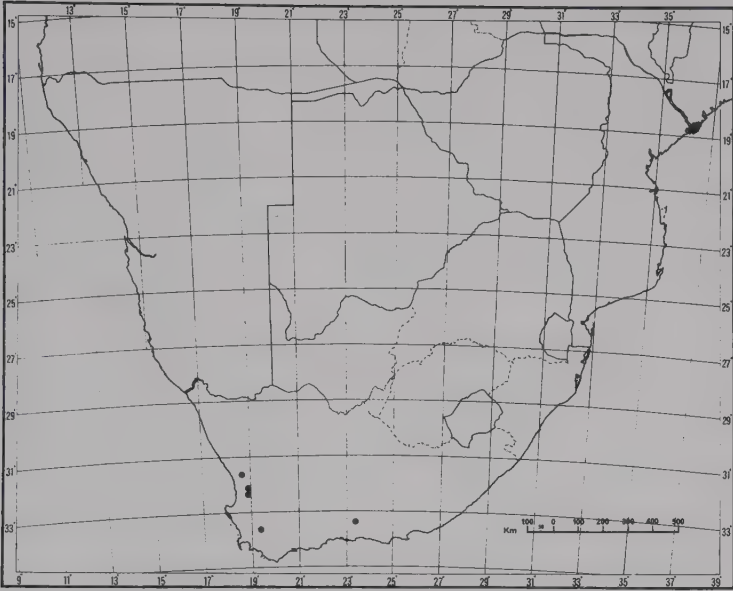


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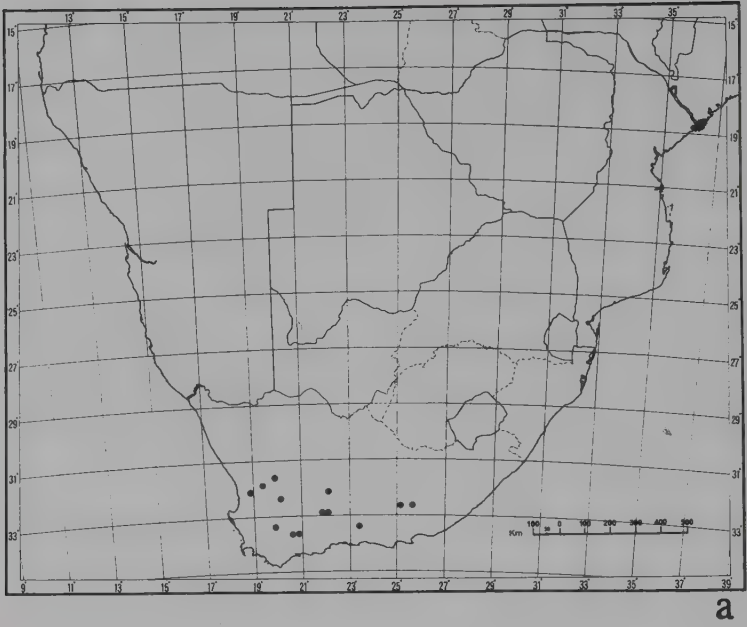
Figure 13. The distributions of the species of *Ceramius* Group 3: (a) *Ceramius nigripennis*; (b) *Ceramius toriger*; (c) *Ceramius braunsi*; (d) *Ceramius jacoti*. All four species forage on Asteraceae.



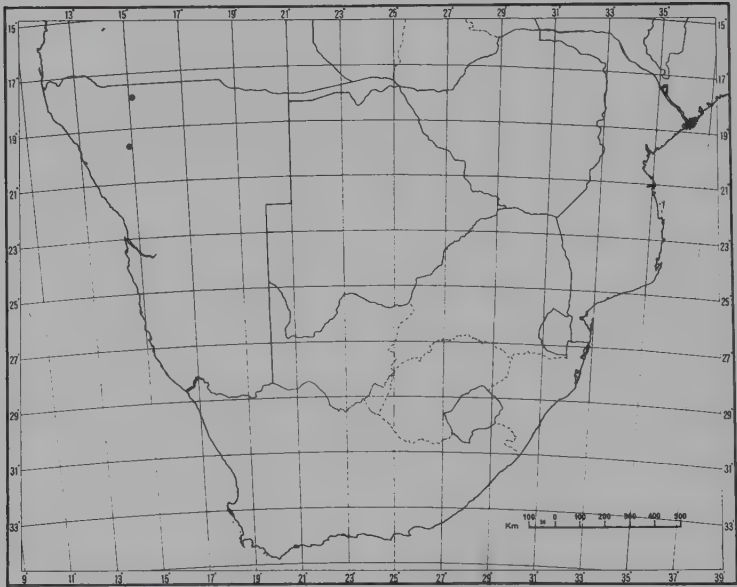
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b

Figure 14. The distributions of the species of *Ceramius* Group 4: (a) *Ceramius beyeri*, which forages on *Mesembryanthema* (Aizoaceae); (b) *Ceramius damarinus*, whose forage plant is unknown.

*Distribution of the pollen wasps compared with that of the bees and of non-masarine aculeate wasps*

Pollen wasps and bees, provisioning with pollen and nectar, fill the same general behavioral niche, so a comparison of their distributions is of particular interest.

Although bees are well represented in the tropics, they are most abundant and diverse in certain warm-temperate, xeric regions of the world (Michener 1979). Furthermore, bees are especially abundant and diverse in the Mediterranean Basin, the Californian Region, and the contiguous xeric areas, but other warm-temperate, xeric areas, like central Chile or the western part of southern Africa, have less rich faunas (Michener 1979). It is perhaps of significance that from a consideration of known species it would appear (even taking into account possible differences in collecting intensity between areas) that pollen wasps are by contrast most diverse in southern Africa. From this region approximately 155 species, all endemic, have been recorded, as compared with about 90 species from the Mediterranean Basin and associated xeric areas, about 32 species from Australia, about 16 species from South America, and about 14 species from North America.

Some bee families have a wider distribution than the pollen wasps, and others have very much more limited distributions. Of note are two families, the Colletidae, which has an entirely Austral distribution with the greatest species diversity in Australia, and the Fideliidae, which is limited to parts of southern Africa and Chile (Michener 1979).

Of marked contrast to the distribution of the pollen wasps is that of the social vespid subfamilies, the paper wasps. Of these all but one genus have species with all or part of their distributions in the tropics (Evans and Eberhard 1970). Other than *Polistes*, few of the nearly 800 polistine species occur north of latitude 30°N (Wenzel 1990).

In southern Africa, whereas the species diversity of the pollen wasps is greatest in the semi-arid areas of the southwest, the species diversity of the social vespids is greatest in the subtropical areas of the northeast. The only three genera of social paper wasps represented are the polistines *Belonogaster*, *Polistes*, and *Ropalidia*. They appear to be species-rich in more tropical parts and in southern Africa display a northeast to southwest gradient of decreasing species numbers.

From available museum records it appears that—although all three genera are represented (albeit in reduced species numbers) in the eastern



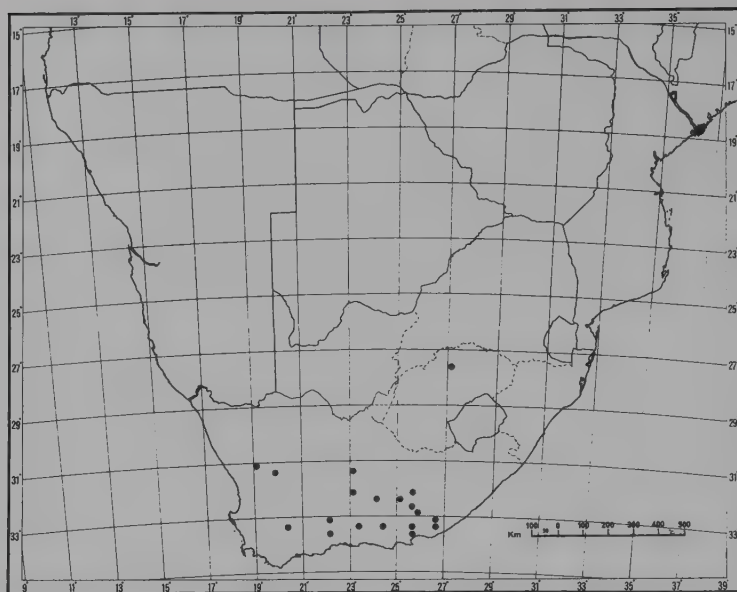
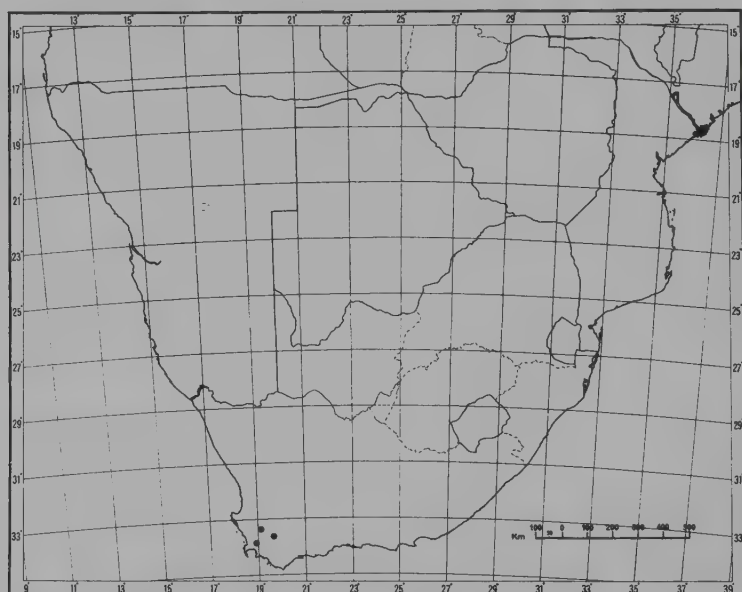
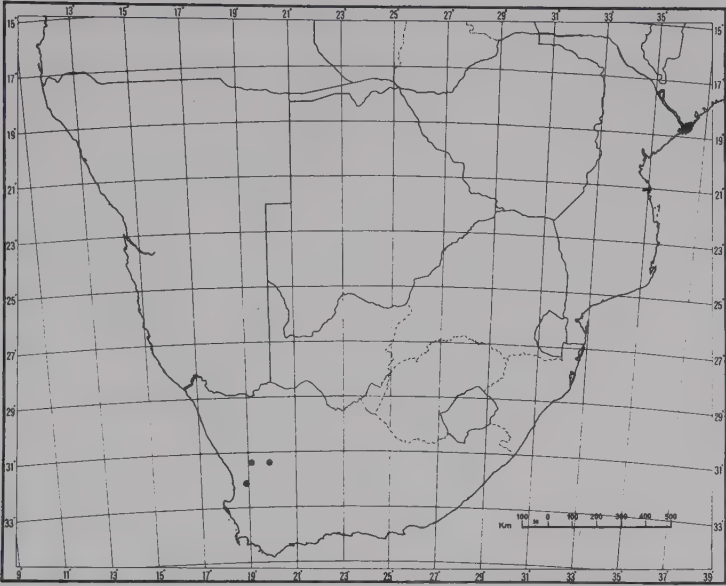


Figure 15. The distribution of the single species of *Ceramius* Group 5, *Ceramius lichtensteinii*, which forages on *Mesembryanthema* (Aizoaceae).

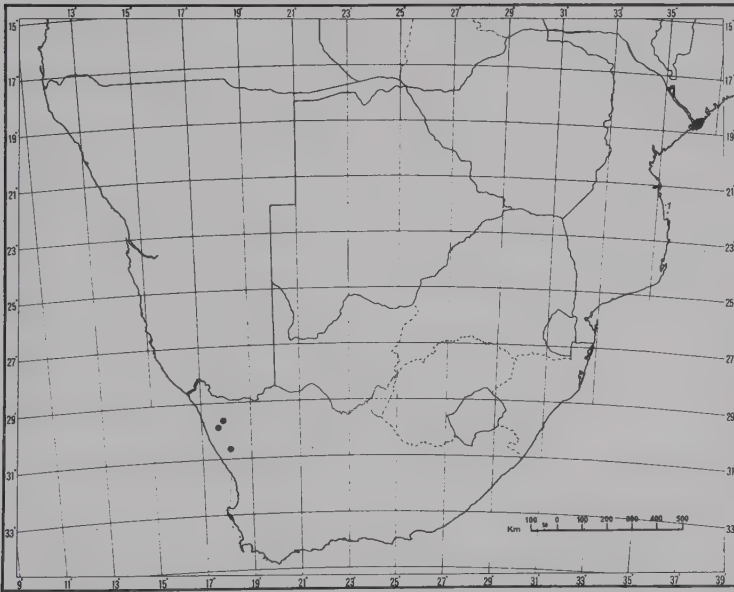


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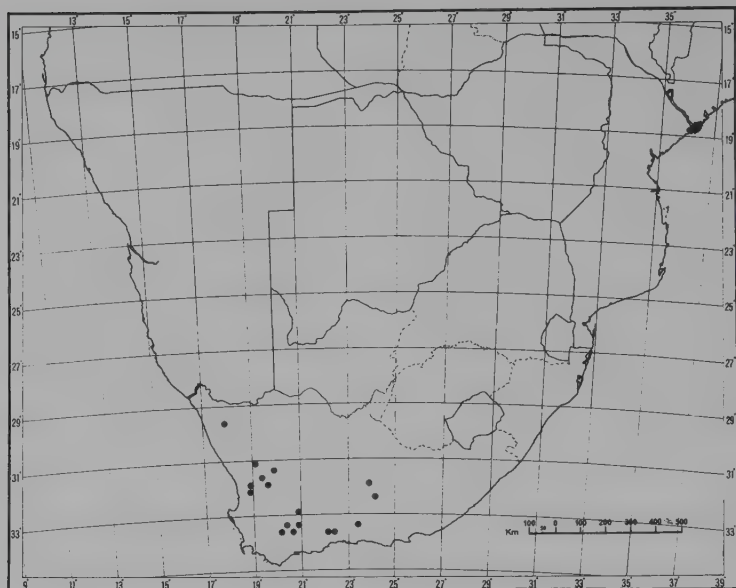
Figure 16. The distribution of the species of *Ceramius* Group 6: (a) *Ceramius caffer*; (b) *Ceramius metanotalis*; (c) *Ceramius rex*. All three species forage on *Asteraceae*.



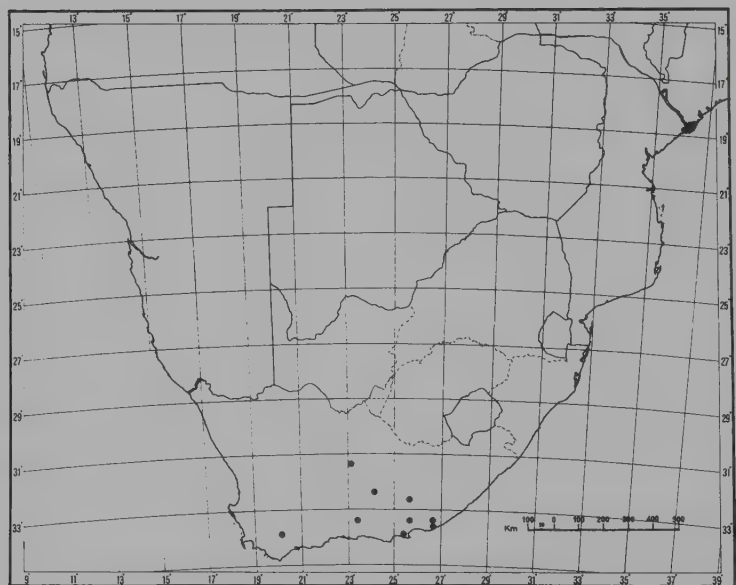
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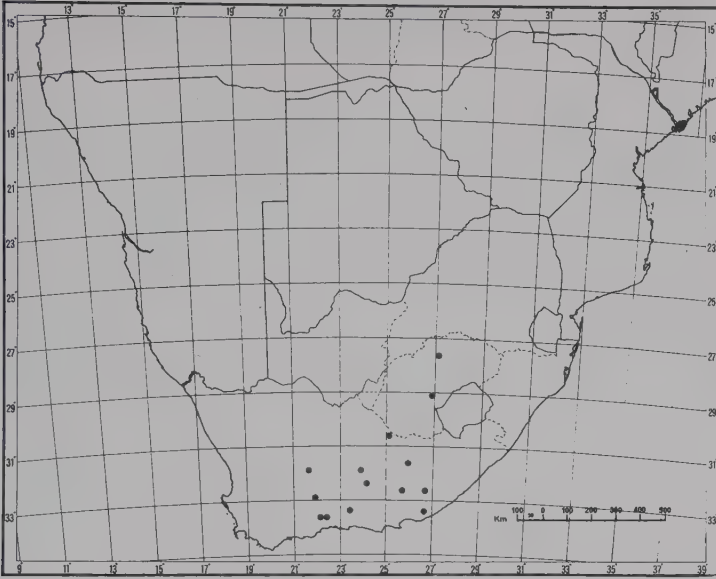


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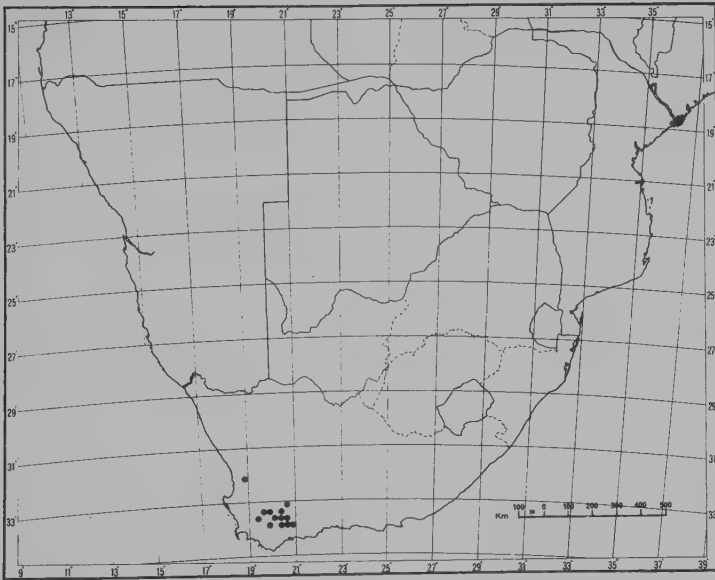


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Figure 17. The distributions of the species of *Ceramius* Group 8: (a) *Ceramius bicolor*; (b) *Ceramius linearis*; (c) *Ceramius capicola*; (d) *Ceramius socius*. All four species forage on *Mesembryanthema* (Aizoaceae).



c



d

Cape, the central Karoo (Colesberg) and westward along the Orange River (Upington, Kakamas and Augrabies), and *Polistes* and *Ropalidia*, at least, extend westward through the southern Karoo (Willowmore, Oudtshoorn, Prince Albert, Ladismith, and Karoo Poort east of Ceres), and *Polistes*, at least, extends along the south coastal regions as far as the Cape Peninsula and the Olifants River Valley (*P. marginalis*)—the polistines are absent from Namaqualand west of the Bokkeveld Escarpment. The contention that polistines are absent from Namaqualand is further supported by the absence of polistines from the flower-visiting lists of Struck (1990). A single *Belonogaster* species collected at Vioolsdrif during the present study is believed to be associated with the Orange River Valley and is not counted as being of Namaqualand.

Whereas the Masarinae has a principally southwestern distribution and the Polistinae has a principally eastern distribution, the other vespidae subfamily present in southern Africa, the Eumeninae, is well represented throughout the region. Indeed the Eumeninae worldwide is widespread and cosmopolitan.

In contrast to genera in other subfamilies, such as *Eumenes* (*sensu* van der Vecht and Carpenter 1990) (Eumeninae), *Polistes* (Polistinae), *Isodontia* (Sphecidae), *Cerceris* (Philanthidae) and *Bembix* (Nyssonidae), to name a few, there are no masarine genera common to all the zoogeographical regions. Indeed, there are no masarine genera shared by more than two zoogeographical regions. It is notable that those genera which are shared, *Ceramius*, *Jugurtia*, *Celonites*, and *Quartinia*, are all Afrotropical/Palaearctic genera. The remaining genera are endemic to single zoogeographical regions. Of these *Masarina*, at least, can be considered to be narrowly endemic. There appear to be no endemic island faunas or odd and highly disjunct distributions such as are found among, for example, the Chrysididae (Kimsey and Bohart 1990).

As the Afrotropical and Palaearctic regions do share species, such as *Prionyx kirbii* (Vander Linden) (Sphecidae) and *Philanthus triangulum* (Fabricius) (Philanthidae), it is of note that no species of masarines are shared between these regions.

To conclude, whereas the adoption of provisioning with pollen and nectar by the sphecoids led to a group, the bees, that has a worldwide distribution including a broad range of biomes, the adoption of provisioning with pollen and nectar by the vespoids led to a group, the pollen wasps,



that although present in five zoogeographical regions, is within those regions markedly restricted to a narrow range of biomes.

Within the Vespidae four types of present distribution can be recognized: widespread worldwide (Eumeninae), worldwide with the highest representation in the tropics (the three social vespid subfamilies as a group); widely distributed but with the highest representation outside the tropics almost entirely in semi-arid and Mediterranean areas (Masarinae); and endemic to a single zoogeographical region (Euparagiinae).

In his consideration of present distributions in relation to past distributions, Carpenter (1993) concluded that the family Vespidae arose before the breakup of Gondwanaland. One reason for this conclusion is that the oldest fossils assignable to the extant subfamily, Euparagiinae, are Cretaceous, as are those of the extinct Priorvespinae. Carpenter also concluded that the biogeographic pattern of the Masarinae, the next subfamily to diversify, corresponds basally to vicariance dating from the earliest stages of the breakup of Gondwanaland, that is, while South America, Africa, and Australia were connected. He suggested that North America may have been reached subsequently by dispersal from the Mediterranean, or that perhaps the connection between these regions (the North American genus *Pseudomasaris* is most closely related to a Mediterranean genus, *Masaris*), also found in other groups of organisms, indicates a more fundamental pattern.

# Flower Associations

Most aculeate wasps and bees, both males and females as adults, visit flowers to obtain nectar for their own nourishment. In addition adult female pollen wasps, like the majority of adult female bees, visit flowers to collect pollen and nectar for provisioning their young. Certain pollen wasps, like certain bees, collect nectar for use in nest construction, and a small minority of bees collect oils.

It has been erroneously stated that among the Aculeata only the bees have elongated proboscises (Kevan and Baker 1983). It is true that short tongues are characteristic of the majority of wasps, however, and although some pollen wasps have relatively short tongues (Table 5 and Fig. 18) most have long tongues, some considerably longer than the wasp's length from the frons to the tip of the abdomen (Table 5 and Fig. 19). Consequently pollen wasps, like long-tongued bees, have the potential to obtain nectar from a wider range of flower forms than do short-tongued wasps and short-tongued bees, most of which are obliged to visit flowers in which the nectar is readily accessible.

### *Review of world pollen wasp/flower associations*

Available flower-visiting records for the pollen wasps of the world have been assembled and are presented in tabular form in Appendix 1.

### Gayellini

Flower-visiting records for the Gayellini are scant and too fragmentary for possible associations to be identified. *Gayella eumenoides* has been recorded

from *Quillaja saponica* (Rosaceae), *Schinus dependens* (Anacardiaceae), and *Baccharis* sp. (Asteraceae), *Gayella araucana* from *Homalocarpus dichotomus* (Apiaceae), and *Gayella reedi* from *Adesmia melanthes* (Papilionaceae).

### Masarini: Paragiina

Flower-visiting records for the Australian group Paragiina are available for seven species of *Paragia* Shuckard, one species of *Ammoparagia* Snelling, two species of *Riekia* Richards and three species of *Rolandia* Richards (Appendix 1)—that is, for 13 of the 32 known species. Of these 13 species 53 percent (including six of the seven species of *Paragia*) have been recorded from the flowers of Myrtaceae and 48 percent from the flowers of Goodeeniaceae (including no species of *Paragia* but the single species of *Ammoparagia*, the two species of *Riekia*, and two of the three species of *Rolandia*), suggesting a strong association with these plants. This suggestion is further strengthened by the fact that the pollen from the provision from nests two species of *Paragia*, *P. tricolor* and *P. decipiens*, was found to be myrtaceous pollen (Houston 1984 and Naumann and Cardale 1987, respectively) and that from nests of *Rolandia angulata* was found to be *Goodenia* pollen (Gess et al. 1995). A further species of *Paragia*, *P. vespiformis*, though recorded from the flowers of Myrtaceae and therefore included in the 53 percent, was, however, found to have provisioned solely with *Acacia* (Mimosaceae) pollen (Houston 1986). This seems to be an unusual preference as there are no other records of masarines provisioning with Mimosaceae. The only other record of a masarine visiting flowers of Mimosaceae, though insects from these flowers have been well collected, is of unusual casual visiting by a male *Jugurtia confusa* (in the Afrotropical Region), a species which regularly provisions solely with the pollen of Aizoaceae.

The preference shown by Australian pollen wasps for Myrtaceae is shared with the Australian bees, which show an overwhelming oligolectic preference for Myrtaceae (Michener 1965).

Two species of *Paragia* have been recorded from Proteaceae, *P. nasuta* together with Myrtaceae and *P. vespiformis* with Mimosaceae and Myrtaceae. These appear to be the only records of visits by masarines to Proteaceae apart from a record by Hattingh and Giliomee (1989) of a "masarid" from flowers of *Leucadendron* in the Afrotropical Region. I have been unable to establish the identity of the wasp as the specimen concerned no longer exists (Hattingh pers. comm., letter of February 27, 1990).

Table 5. Body length, tongue length, and the ratio of tongue length to body length for some Australian and southern African masarines.

Species	Sex	N	A	B	Ratio $B:A$
			Average body length (mm)	Average tongue length (mm)	
<i>Paragia nasuta</i>	F	3	14.39	2.07	0.14
<i>P. odyneroides</i>	F	1	10.42	1.48	0.14
<i>Riekia confluens</i>	F	9	9.44	2.60	0.28
<i>R. nocatunga</i>	F	4	8.75	2.13	0.24
<i>Rolandia angulata</i>	F	4	9.94	2.61	0.26
<i>Ceramius bicolor</i>	F	4	10.83	2.96	0.27
	M	2	10.50	2.92	0.28
<i>C. braunsi</i>	F	10	17.28	4.70	0.27
<i>C. caffer</i>	F	1	17.00	5.41	0.32
<i>C. capicola</i>	F	8	10.90	2.54	0.19
<i>C. cerceriformis</i>	F	4	17.33	4.08	0.24
	M	6	17.06	4.46	0.26
<i>C. chypeatus</i>	F	10	15.43	2.98	0.19
	M	10	15.48	3.18	0.21
<i>C. lichtensteinii</i>	F	6	17.78	5.56	0.31
	M	4	17.83	5.54	0.31
<i>C. metanotalis</i>	F	4	19.34	6.23	0.32
	M	2	19.83	5.75	0.29
<i>C. micheneri</i>	F	3	13.61	2.75	0.20
	M	2	12.50	2.38	0.19
<i>C. nigripennis</i>	F	6	14.86	4.08	0.27
	M	7	15.17	4.57	0.30
<i>C. rex</i>	F	1	20.86	5.83	0.28
<i>C. richardsi</i>	F	1	14.33	2.92	0.20
<i>C. socius</i>	F	9	14.30	4.22	0.30
	M	7	13.74	4.02	0.29
<i>C. toriger</i>	F	9	15.33	5.56	0.36
	M	2	15.33	5.21	0.34
<i>Jugurtia braunsi</i>	F	8	9.92	3.69	0.37
<i>J. braunsiella</i>	F	3	11.17	4.11	0.37
<i>J. confusa</i>	M	4	10.08	4.23	0.42

Table 5 (continued)

Species	Sex	N	A Average body length (mm)	B Average tongue length (mm)	Ratio B:A
<i>Masarina familiaris</i>	F	8	10.09	3.54	0.35
	M	5	8.80	3.28	0.37
<i>M. mixta</i>	F	10	8.85	3.71	0.42
	M	8	7.45	2.92	0.39
<i>Celonites bergenwabliae</i>	F	3	7.56	4.28	0.57
	M	7	6.56	3.35	0.51
<i>C. capensis</i>	F	7	8.89	5.71	0.64
	M	2	8.75	5.04	0.58
<i>C. clypeatus</i>	F	10	8.80	5.68	0.66
	M	2	7.63	4.96	0.65
<i>C. latitarsis</i>	F	3	8.33	4.33	0.52
	M	2	6.91	3.42	0.51
<i>C. peliostomi</i>	F	20	6.76	4.73	0.70
	M	4	7.08	4.17	0.59
<i>C. wahlenbergiae</i>	F	6	7.47	4.29	0.57
	M	6	6.88	3.40	0.49
<i>Quartinia parcepunctata</i>	F	1	5.53	2.25	0.42
<i>Quartinioides laeta</i>	F	3	3.69	4.88	1.32
<i>Q. sp. F</i>	F	2	3.94	5.40	1.32

Source: Measurements taken from pinned dried specimens with tongues extended. (Vouchers in Albany Museum collection.)

One female of *Paragia oligomera* has been recorded from the flowers of *Reglia ciliata* (Bromeliaceae). No other flower-visiting records are available for this wasp and there appear to be no other records of any masarines visiting Bromeliaceae, so it is not possible at present to evaluate this record.

All the above records are for Western Australia, New South Wales, or southern Queensland, making the record from the Northern Territory of four female and three male *Rolandia borreriae* from the flowers of *Borreria exserta* (Rubiaceae) of particular interest. The size of the sample and the lack of other flower-visiting records for this species does suggest a possible association with Rubiaceae, a family of plants for which there appear to be



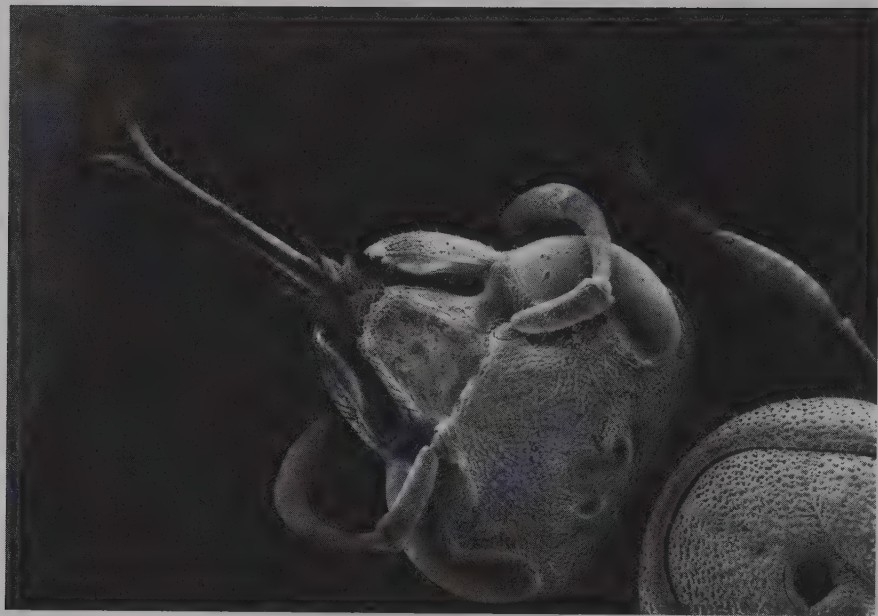


Figure 18. *Ceramius clypeatus*, an example of a relatively short-tongued masarine wasp, dorsal view of head with tongue extended ( $\times 19$ ).



Figure 19. *Quartinioides laeta*, an example of a relatively long-tongued masarine wasp, dorsal view with tongue extended ( $\times 17$ ).

no other records of masarine visits. It should be noted, however, that the Rubiales are closely related to the Asterales (Cronquist 1988), an order of plants strongly favoured by a high percentage of the southern African masarines.

## Masarini: Masarina

### *Ceramius* Latreille

The available flower-visiting records for Palaearctic *Ceramius* species (*Ceramius* groups 1 and 7) (Appendix 1) are few and casual and do not indicate any preferences. On the other hand, flower-visiting records are available for 18 of the 19 described southern Afrotropical *Ceramius* species (groups 2–6 and 8) (Appendix 1). Of these 18 species, 50 percent have been recorded from the flowers of Asteraceae, 44 percent from the flowers of Aizoaceae, and 22 percent from the flowers of Papilionaceae. That the percentages for flower families visited is in excess of 100 percent is explained by records of occasional visits by some species to plants of families other than those preferred. Such visits appear to be for nectar only. For example, we have occasionally collected females of *Ceramius braunsi*, a species showing a clear preference for Asteraceae, from flowers of *Aspalathus spinescens* (Papilionaceae). However, I examined microscopically pollen from the crop of such a female and found it to be entirely derived from flowers of Asteraceae.

Other plants recorded as being occasionally visited by *Ceramius* species in southern Africa are *Wahlenbergia* (Campanulaceae) by *Ceramius socius* and *Blepharis* (Acanthaceae) by *Ceramius lichtensteinii*. Visits to *Wahlenbergia* flowers are not unusual for some other masarine genera: they are the known preferred flowers of some southern African species of *Celonites* and *Quartinia* and a species of *Masarina*, and are occasionally visited by *Jugurtia*. Flowers of Acanthaceae are not otherwise visited by pollen wasps, though flowers of the closely related family Scrophulariaceae are the preferred flowers of some species of southern African *Celonites* and *Quartinoides* and of the North American genus *Pseudomasaris*.

Pollen from provision obtained from 14 *Ceramius* species was for each species derived from a single plant family, which indicates that the genus *Ceramius* is markedly oligolectic and makes it possible to recognize clear associations (Table 6).

Table 6. *Ceramius* species/forage plant associations.

Species group	Species	Forage plant taxa
Group 2A	<i>cerceriformis</i> <i>peringueyi</i>	Aizoaceae: Mesembryanthema Aizoaceae: Mesembryanthema (foraging records only)
Group 2B	<i>clypeatus</i>	Papilionaceae: <i>Aspalathus</i>
Uncertain	<i>micheneri</i>	Papilionaceae: <i>Aspalathus</i>
Group 3	<i>nigripennis</i> <i>jacoti</i> <i>braunsi</i> <i>toriger</i>	Asteraceae Asteraceae Asteraceae Asteraceae
Group 4	<i>beyeri</i>	Aizoaceae: Mesembryanthema (foraging records only)
Group 5	<i>lichtensteimii</i>	Aizoaceae: Mesembryanthema
Group 6	<i>rex</i> <i>metanotalis</i> <i>caffer</i>	Asteraceae Asteraceae Asteraceae (foraging record only)
Group 8	<i>capicola</i> <i>linearis</i> <i>bicolor</i> <i>socius</i>	Aizoaceae: Mesembryanthema Aizoaceae: Mesembryanthema Aizoaceae: Mesembryanthema Aizoaceae: Mesembryanthema

A high percentage of species associated with Asteraceae and Aizoaceae is shared with southern African *Jugurtia* and the *Quartinia*, *Quartinoides*, and *Quartiniella* complex.

### *Ceramiopsis* Zavattari

There appear to be no flower-visiting records for the Neotropical genus *Ceramiopsis*.

### *Trimeria* Saussure

Available flower-visiting records for the Neotropical genus *Trimeria* are few both in number of species, four, and in instances (Appendix 1). Associations with Portulacaceae, Verbenaceae, and Boraginaceae are, however,

indicated. Visits to Malvaceae and Asteraceae though recorded are too few for evaluation. Portulacaceae though not otherwise recorded as a family visited by pollen wasps is, interestingly, closely related to Aizoaceae, a family so much favored by pollen wasps in southern Africa. Verbenaceae and Boraginaceae are closely related families though Verbenaceae is not otherwise known as a family visited by pollen wasps. Boraginaceae appears to be favored by *Celonites* and possibly *Masaris vespiformis* in the Palearctic. A single visit by a male *Celonites capensis* to Boraginaceae has been recorded from southern Africa.

### *Microtrimeria* Bequaert

There appear to be no flower-visiting records for the Neotropical genus *Microtrimeria*.

### *Masaris* Fabricius

Flower-visiting records for the Palearctic genus *Masaris* are scant (Appendix 1). A possible association between *Masaris vespiformis* and *Echium* (Boraginaceae) is indicated by its having been collected on flowers of these plants in both Algeria and Egypt. There is, however, a record of it from Lamiaceae in Israel. The record of *Masaris carli* from *Tamarix* (Tamaricaceae) in Kazakhstan is of interest, if taken together with the record of casual visiting of *Tamarix* by *Pseudomasaris edwardsii* in North America.

### *Pseudomasaris* Ashmead

Flower-visiting records are available for 13 of the 14 described species of the Nearctic genus *Pseudomasaris* (Appendix 1). Of these 92 percent have been recorded from flowers of Hydrophyllaceae of the genera *Phacelia* and *Eriodyction* and 31 percent have been recorded from flowers of Scrophulariaceae, in particular of the genus *Penstemon*. That the sum of the percentages for flower families visited, given above, is in excess of 100 percent is explained by records of visits by some species to both families. Fifteen other flower families are listed as being visited, but sizes of samples and observations of those (Richards 1963b; Torchio 1970, 1974) who have made studies of *Pseudomasaris* flower visiting and nesting behavior indicate that visits to these families are casual in nature. This supports Cooper's

(1952) conclusion that *Pseudomasaris* species are in the main oligolectic, favoring principally *Phacelia* or *Penstemon*. Tepedino (1979), basing his argument on field observations of his own, questioned Cooper's assertion with regard to *P. vespoides* and expressed the opinion that Cooper had acted arbitrarily in discarding the records of Clements and Long (1923) and Hicks (1927). However, he does not comment on Torchio's (1974) study of the pollination of *Penstemon* by this wasp.

### *Jugurtia* Saussure

Flower-visiting records are available for eight southern African species and three Palaearctic species of *Jugurtia* (Appendix 1). Six of the eight southern African species and one Palaearctic species have been recorded from flowers of Asteraceae and four southern African species have been recorded from Aizoaceae. For one of the latter species, *J. confusa*, I obtained provision. The pollen from this provision was derived solely from flowers of Aizoaceae, suggesting that *J. confusa* at least is oligolectic. Two of the other species, *J. braunsi* and *J. duplicata*, have been recorded in addition from Asteraceae and the former also from Campanulaceae (*Wahlenbergia pilosa*). Regrettably its provision is not known. Records for the Palaearctic species are scant, precluding evaluation. The records of visits to Apiaceae are remarkable, as wasps and bees visiting Apiaceae in southern Africa have been well collected and there have been no records of visits by pollen wasps.

### *Masarina* Richards

Flower-visiting records are available for all the known species of the southern Afrotropical genus *Masarina* (Appendix 1). Four of the five species have been recorded from Papilionaceae (Fabaceae). The fifth is known only from *Hermannia disermifolia* of the family Sterculiaceae (Malvales), with which it is closely associated. This appears to be the only record of a pollen wasp visiting flowers of this family. There are, however, records of casual visiting of flowers of Malvaceae (Malvales) by *Jugurtia* in Algeria, *Trimeria* in South America, and *Pseudomasaris* in North America. Of those species visiting Papilionaceae, *Masarina familiaris* and *Masarina hyalinipennis* can be said to be closely associated with Papilionaceae of the Cape Group of the Crotalariaeae, as they have been collected repeatedly from widely separated sites from flowers of this group but from no other.



Furthermore, pollen examined from provision of *M. familiaris* was also all from this group. *Masarina mixta* on the other hand has been recorded many times from *Wahlenbergia* (Campanulaceae), whereas only one female has been collected from Papilionaceae and one other has been collected from Asteraceae. These appear to be casual visits and it therefore seems probable that it, like some of the southern Afrotropical *Celonites* species, is associated almost entirely with *Wahlenbergia*.

### *Celonites* Latreille

Flower-visiting records are available for 10 species from the southern Afrotropical Region and nine species from the Palaearctic Region (Appendix 1). Of the Afrotropical species, six species have been recorded from flowers of Scrophulariaceae, four species from flowers of Campanulaceae and one species from flowers of the closely related family Lobeliaceae, five species from flowers of Asteraceae, and three species from flowers of Aizoaceae.

Of the six species recorded from Scrophulariaceae, three have been collected abundantly from widely separated localities solely from *Apotosimum* and *Peliostomum*, indicating a close association between these pollen wasps and these plant genera, a preference shared with some species of *Quartinioides*. The remaining three species recorded from Scrophulariaceae were collected on *Polycarena*, to which they seem to be casual visitors. Three of the species visiting Campanulaceae are closely associated with *Wahlenbergia* species although two, at least, are not restricted to them. The fourth appears to be a casual visitor. The species visiting Lobeliaceae has been collected only from *Lobelia linearis* but records are too few for an evaluation of the closeness of the association to be made. Of the species visiting Asteraceae, only one species (or possibly two) has a close association with these plants and the remainder are casual visitors.

Eight of the nine Palaearctic species have been collected from Boraginaceae, a family known to be visited only casually by one species of southern Afrotropical *Celonites*. Though the collecting records are few the number of species involved does suggest a possible association, a preference indicated for some species of *Trimeria*. Two species have been collected from Lamiaceae and Schremmer (1959) suggests a close association by *Celonites abbreviatus* with this family. This is of particular interest, as in the southern Afrotropical Region no pollen wasps have been found



to be associated with this family even as casual visitors. However, in the Palaearctic *Ceramius* and *Masaris* and in the Nearctic *Pseudomasaris* have been recorded as casual visitors.

*Quartinia* Ed. André, *Quartinoides* Richards, and *Quartiniella* Schulthess Group

Flower-visiting records are available for 17 species of *Quartinia*, 37 species of *Quartinoides*, and one species of *Quartiniella* in the southern Afrotropical Region and for 11 species of *Quartinia* in the Palaearctic Region (Appendix 1).

As these genera are very closely related (Carpenter, in prep.,b) they will be treated as a group. Of the 55 southern Afrotropical species 55 percent have been recorded from Aizoaceae, 33 percent from Asteraceae, 16 percent from Campanulaceae, and 11 percent from Scrophulariaceae. In addition Wharton (1980) recorded an undescribed species of *Quartinoides* foraging abundantly on *Zygophyllum simplex* (Zygophyllaceae).

Exceptional is the record of a good sample of *Quartinoides antigone* from *Aloe striata* (Liliaceae). The only other record of a pollen wasp visiting Liliaceae, indeed any "monocot," is a casual visit by a species of *Pseudomasaris* to *Yucca*.

Records for most species are insufficient to indicate how many species can be expected to be associated with a single family of plants. Certainly provision from *Quartinia vagepunctata* was all derived from flowers of Asteraceae, the single recorded visits to Aizoaceae and Papilionaceae seemingly representing casual visiting.

Of the 11 Palaearctic species, the six species from North Africa and the single species from Iran have all been recorded solely from Asteraceae, and the three species from the Canary Islands from Asteraceae with other families in addition. The species from Samarkand and Tadzhikistan (as Tadjikistan in Richards 1962) has been recorded from Chenopodiaceae, a family closely related to Aizoaceae.

### *Pollen wasp/forage plant associations in relation to pollen wasp distributions*

It is clear from the foregoing review of pollen wasp/flower associations that, where satisfactory foraging and provisioning records are available for

pollen wasps, oligolecty (collection of pollen from flowers of plants of a single family or even genus) and narrow polylecty (collection of pollen from plants of a limited range of families) are the rule. Broad polylecty (collection of pollen from a wide range of families) in Masarinae seems to be the exception. That some of the flowers favored by pollen wasps are themselves generalists, for example Asteraceae, and others specialists, for example Scrophulariaceae, is not surprising when one realizes that the evolutionary factors favoring specialist or generalist pollinators are not necessarily the same as those favoring specialist or generalist flowers (Cruden 1972; Heinrich 1979; Proctor 1978). Indeed Moldenke (1979) observed that a one-to-one bee/plant relationship is rarely observed in nature. Rather, there is a tremendous overlap in the forage plant preferences of specialist bees.

The high incidence of oligolecty in pollen wasps is in accord with the statement of Michener (1979) with regard to bees—that oligolecty is highest in the arid, warm-temperate areas where climatic conditions lead to simultaneous flowering of many kinds of plants. Indeed Emlen (1973) concluded that, if resources are predictable and their density or quality is high, specialization is favored. I (Gess 1992b) have obtained some measure of the comparative diversity of flowers visited by masarine wasps and bees in the semi-arid areas of southern Africa. My analysis was based on more than 7,000 records of flower visits by more than 616 species of aculeate wasps and bees to 35 families of plants. Fourteen flower families were visited by masarine wasps and 30 by bees. I obtained some measure of the percentage diversity of choice at the specific level

$$D = \frac{a - b}{b} \times 100$$

where  $a$  = the sum of the number of species recorded visiting each of the flower families and  $b$  = the number of species of flower visitors.  $D = 43.0$  percent for pollen wasps and 95.6 percent for solitary bees. These percentages indicate a markedly narrower diversity of flower choice at the specific level by pollen wasps overall than by solitary bees. Marked variations in diversity of flower visiting between families of bees are, however, apparent. The percentage diversity of choice at the specific level for the individual bee families (excluding Andrenidae and Fideliidae, for which there were too few records) was: 38.1 percent for Colletidae, 121.2 percent for Halictidae, 44.4 percent for Melittidae, 73.6 percent for Megachilidae,

Table 7. Major plant preferences of Masarini. Possible preferences, suggested by number or nature of records, are listed in square brackets.

Masarine taxon	Region	No. of spp. with data	Plant taxon
Paragiina <i>Paragia</i> , <i>Metaparagia</i> , <i>Riekia</i> , <i>Rolandia</i> , and <i>Ammoparagia</i>	Australian	14	Myrtaceae (Myrtales) 47% Goodeniaceae (Campanulales) 47% Mimosaceae (Fabales) [Rubiaceae (Rubiales)] [Bromeliaceae (Bromeliales)]
Masarina <i>Ceramius</i>	S Afrotropical	18	Asteraceae (Asterales) 50% Aizoaceae (Caryophyllales) 44% Papilionaceae (Fabales) 22% [Resedaceae (Capparales)] [Plumbaginaceae (Plumbaginales)]
<i>Ceramiopsis</i>	Palaeartic	2	Unknown
<i>Trimeria</i>	Neotropical	4	Unknown
<i>Microtrimeria</i>	Neotropical	4	Verbenaceae (Lamiales) [Boraginaceae (Lamiales)] [Portulacaceae (Caryophyllales)]
<i>Masaris</i>	Palaeartic	2	Unknown
<i>Pseudomasaris</i>	Nearctic	13	[Boraginaceae (Lamiales)] [Lamiaceae (Lamiales)] [Tamaricaceae (Violales)]
<i>Jugurtia</i>	S Afrotropical	7	Hydrophyllaceae (Solanales) 92% Scrophulariaceae (Scrophulariales) 31% [Boraginaceae (Lamiales)] [Ranunculaceae (Ranunculales)] [Asteraceae (Asterales)]
	Palaeartic	3	Asteraceae (Asterales) Aizoaceae (Caryophyllales) [Campanulaceae (Campanulales)] [Asteraceae (Asterales)] [Apiaceae (Apiales)]
<i>Masarina</i>	S Afrotropical	5	Papilionaceae (Fabales) Sterculiaceae (Malvales)

Table 7 (continued)

Masarine taxon	Region	No. of spp. with data	Plant taxon
<i>Celonites</i>	S Afrotropical	10	Asteraceae (Asterales)
			Aizoaceae (Caryophyllales)
			Scrophulariaceae (Scrophulariales)
			Campanulaceae (Campanulales)
			Lobeliaceae (Campanulales)
			[Geraniaceae (Geraniales)]
<i>Quartinia</i> , <i>Quartinioides</i> , and <i>Quartiniella</i>	Palaeartic	9	Lamiaceae (Lamiales)
			[Boraginaceae (Lamiales)]
			Aizoaceae (Caryophyllales) 55%
			Asteraceae (Asterales) 33%
			Campanulaceae (Campanulales) 16%
			Scrophulariaceae (Scrophulariales) 11%
<i>Quartinia</i>	Palaeartic	11	[Liliaceae (Liliales)]
			[Zygophyllaceae (Sapindales)]
			[Asteraceae (Asterales) 10 spp.]
			[Chenopodiaceae (Caryophyllales) 1 sp.]
			[Frankeniaceae (Caryophyllales) 2 spp.]

and 150.8 percent for Anthophoridae. This indicates a similar percentage diversity of choice for Masarinae, Colletidae, and Melittidae and narrower diversity of choice for Masarinae compared with Halictidae, Megachilidae, and Anthophoridae.

In a study of ecosystem organization in the semi-arid areas of Chile and California, Moldenke (1979) found that the majority of bee species are specialist feeders upon a particular genus, family, or similar limited array of closely related plant taxa. In addition, he pointed out that along the Pacific Coast and in the Sonoran Desert of the United States, there are nearly 2,000 species of bees, of which nearly 60 percent or 1,200 species are specialized feeders. However, of these 1,200 specialists at least 950 frequent taxa of only about 45 plant genera. This together with my analysis for southern Africa is of interest when one considers the small range of plant groups visited by the pollen wasps in any one zoogeographical region (Table 7).

Major marked foraging preferences are shown by the Australian pollen wasps for Myrtaceae (Myrtales) and Goodeniaceae (Campanulales), by the

Nearctic genus *Pseudomasaris* for Scrophulariaceae (Scrophulariales) and Hydrophyllaceae (Solanales), and by the Afrotropical pollen wasps (based on data for 92 species representing all seven genera) for Aizoaceae (predominantly Mesembryanthema) (Caryophyllales) (45 percent), Asteraceae (= Compositae) (Asterales) (41 percent), Campanulaceae (Campanulales) (18 percent), Scrophulariaceae (13 percent), and Papilionaceae (= Fabaceae) (Fabales) (7 percent). Data available for the Neotropical and Palaearctic species are inadequate for definite associations to be recognized, however, associations are indicated for one species of *Trimeria* with Verbenaceae (Lamiales) in the Neotropical Region, and for *Quartinia* species with Asteraceae in the Palaearctic Region.

The Myrtaceae (Myrtales), although relatively widespread, show marked species diversity in Australia. The association of some Australian pollen wasps with this family stands out as distinct. If one considers that the Myrtales are members of the subclass Rosidae, a connection can be found with known pollen wasp associations with Fabales also of the subclass Rosidae: with Mimosaceae by a single species in Australia, and with Papilionaceae by 7 percent of southern African species and casually by a Palaearctic species and a Nearctic species.

The three southern African species of *Ceramius* associated with the genus *Aspalathus* (Papilionaceae) are strikingly restricted in their distributions. The species of *Aspalathus* with which they are associated are all species with restricted distributions although somewhat less so than their pollen wasp visitors. *Masarina familiaris* and *Masarina hyalinipennis*, associated with *Aspalathus*, *Lebeckia*, and *Wiborgia*, are less restricted—both have been recorded from Namaqualand and the Olifants River Valley and *M. familiaris* in addition eastward to Willowmore in the southern Karoo. They have therefore together been recorded from about half the range of the genus *Aspalathus*, which extends eastward beyond the semi-arid areas into Natal, the southwestern third of the range of the genus *Lebeckia*, and most of that of *Wiborgia* (van Wyk 1991) (Fig. 20).

The marked preference for Asteraceae (Asterales) by many Afrotropical species can be linked to the apparent preference by some species of masarines for this family in the Palaearctic Region. It seems surprising, however, that it is only within the Afrotropical and Palaearctic regions that the family Asteraceae has been exploited by pollen wasps. This family is widespread and there was a rapid production of many genera and species in response to the expansion of semi-arid and sub-humid habitats (Raven



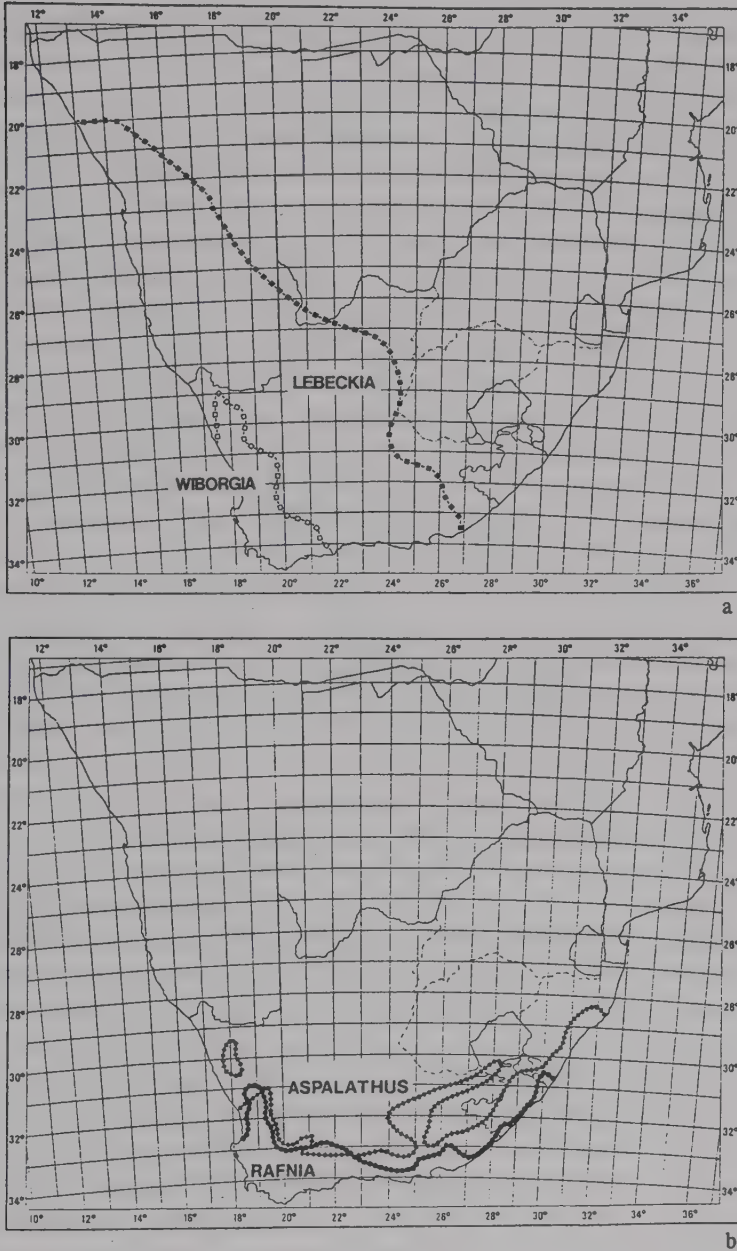


Figure 20. Approximate geographic distribution of genera of the Cape Group of the Crotalariaeae (from van Wyk 1991).



and Axelrod 1974). There is therefore a rich diversity of "composites" within the distribution ranges of the masarines worldwide.

It is noteworthy that the Asterales are relatively closely allied to the Campanulales in the subclass Asteridae (Cronquist 1988). A significant number of Australian pollen wasps is associated with Goodeniaceae and Afrotropical masarines with Campanulaceae, both families of the Campanulales. The Goodeniaceae show their greatest species diversity in Australia, especially in the southwest (Cronquist 1988). The family Campanulaceae is relatively widespread, however, the genus *Wahlenbergia*, with which at least 18 species of southern African pollen wasps are associated, is in the main African (Thulin 1975). Of the 200 species nearly 150 species occur in southern Africa, the greatest concentration of species being in the southwest. It is notable that in this region deep-flowered *Wahlenbergia* species are almost invariably attended by pollen wasps.

Also included in the Asteridae and of importance to the pollen wasps are the Scrophulariales, the Solanales, and the Lamiales. The Nearctic pollen wasps fall into two groups, one markedly associated with Scrophulariaceae (Scrophulariales) and the other with Hydrophyllaceae (Solanales). Also markedly associated with Scrophulariaceae are 13 percent of the Afrotropical masarine species. One casual collecting record for a pollen wasp on Scrophulariaceae in the Palaearctic Region has been noted. Pollen wasps have been collected from all three families of the Lamiales: Lamiaceae (= Labiatae) in the Nearctic and the Palaearctic regions; Boraginaceae in the Nearctic, Neotropical, Palaearctic, and Afrotropical regions; and most notably Verbenaceae in the Neotropical Region.

In western North America the species of *Pseudomasaris* fall into two groups, one associated with *Penstemon* (Scrophulariaceae) and the other with *Phacelia* (Hydrophyllaceae). *Penstemon* and *Phacelia* are principally North American genera with the greatest concentration of species in the west (Willis 1966).

In southern Africa three species of *Celonites* are associated with *Aptosimum* and *Peliostomum* (both Scrophulariaceae). *Aptosimum* and *Peliostomum* are African genera, the majority of species being southern African and being concentrated mostly in the western dry regions (Dyer 1975). Two, at least, of the species of *Celonites* associated with these plants are widely distributed throughout their range.

The high percentage of Afrotropical species associated with Aizoaceae cannot be matched in any other region. Several Palaearctic species have,



Figure 21. The distribution and frequency of the 116 recognized genera of *Mesembryanthema* (from Hartmann 1991). A = Albany centre; G = Gariep centre; K = Little Karoo centre; V = Vanhynsdorp centre; W = Pofadder centre.

however, been collected from the flowers of *Chenopodiaceae* and one Neotropical species has been collected from *Portulacaceae*, both, like the *Aizoaceae*, families of the *Caryophyllales*.

Of note is the striking similarity between the overall distribution and the areas of diversity richness of the Afrotropical pollen wasps (Fig. 7) and the *Mesembryanthema* (Fig. 21) (from Hartmann 1991), particularly the correspondence of nodes of species richness designated by Hartmann as Gariep centre, Vanhynsdorp centre, and Little Karoo centre, and of areas of relatively high diversity of southern Namibia and the southwestern Cape. There is similarly a correspondingly low diversity in the Great Karoo with limited areas of higher diversity near Bloemfontein and Maseru.

In conclusion, pollen wasps as a group favor a relatively narrow range of plant taxa. If one considers major plant preferences by zoogeographical region, however, marked distinctions are apparent. Relatedness of plant

preferences between zoogeographical regions becomes more apparent when relatedness of the plant taxa is considered. Furthermore, there are marked correlations in areas of species richness between pollen wasps and their forage plants. The oligolectic species though dependent on the presence of their forage plants are, in some instances at least, more narrowly endemic than their forage plants. This corroborates Michener's (1979) observation that plants commonly range more widely than their oligolectic visitors.

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## CHAPTER 4

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# Life History

### *Life cycle*

Pollen wasps exhibit the usual holometabolous development of egg, larva, pupa, adult. The egg, larval, and pupal stages are passed enclosed within a cell with earthen walls. Cells either terminate a shaft in a multicellular nest excavated in the ground or in vertical earthen banks or are constructed aerially on stones or plant stems or in a pre-existing cavity, with water, nectar, or self-generated silk being the bonding agents (Chapter 5).

No pollen wasps have been found to be nest parasites. The unusual form of the abdomen which gives *Celonites* the ability to roll itself in the manner of the Chrysididae led to an assumption that it would be found to be a nest parasite of other Hymenoptera in chrysidid manner. Rossi (1790) placed *Celonites abbreviatus* (Villers) (as *Chrysis dubia* Rossi) in the Chrysididae. The same species was believed by Saussure (1854) to be parasitic. In 1869, however, Lichtenstein recorded that *Celonites abbreviatus* constructs its own cells. Despite this Friese (1926) held the opinion that the morphology and rolling behavior indicated a parasitic way of life like that of the chrysidids. No evidence has been found to support this opinion. On the other hand, nest construction has been recorded for seven, possibly eight, species of *Celonites*.

The formation of nesting aggregations is usual for ground-nesting species. It could result from the congregation of unrelated nesting individuals or from a tendency for individuals to nest in close proximity to their natal nests. The latter, at least, is indicated—I have found reused multicellular nests with multiple emergences occupied by a single female

associated with new nests in most species of *Ceramius* and one species of *Masarina* (Gess and Gess 1986, 1988a, 1988b, 1990).

The majority of nesting studies indicate that nest construction, egg laying, and provisioning are performed by a single female per nest, but nest sharing has been alleged by Zucchi et al. (1976) for *Trimeria howardi* and by Brauns (1910) for *Ceramius lichtensteinii*. Nest sharing by *C. lichtensteinii* is certainly not habitual—Fred and I found no evidence of it in the population of this species studied by us (Gess and Gess 1980). As nests are reused it is conceivable, however, that with a breakdown in territorial aggression nest sharing could occur. Some flexibility in the behavior of this species has been noted by us—mud pellets discarded during nest excavation were dropped outside the limits of the nesting aggregation at one locality whereas at other localities they were dropped among the nests.

Pollen wasp eggs can be seen to be relatively large for wasps' eggs but relatively small compared with bees' eggs, if the ratio of egg length to female length is compared (1:5.4, 1:3.3, and 1:1.5 respectively for a random sample of non-masarine wasps, masarines, and bees). Masarines oviposit into an empty cell before provisioning takes place, as do all the other vespoids and some of the nyssonines. They therefore differ from the majority of aculeate wasps and the majority of bees, which oviposit onto the provision in a partially or fully provisioned cell. In common with the majority of aculeate wasps and bees, a single egg is laid in each cell. It is positioned at the blind end of the cell, either lying free as in the ground-nesting *Paragia*, *Ceramius*, and *Jugurtia* or glued to the wall at the blind end in *Masarina familiaris* nesting in vertical banks and in the aerial nesting *Gayella* and *Pseudomasaris*.

According to Ferton (1901), the egg of *Ceramius tuberculifer* is deposited only provisionally at the bottom of the cell. After the cell has been provisioned with a firm pollen loaf of characteristic retort shape (Ferton 1901, Plate 1, Fig. 10), the mother moves the egg onto the neck of the "retort." In this position the little larva is alleged to begin feeding. Much has been made of Ferton's assertions by Malyshev (1968), who in his chapter on the genesis of bees has based his "Secondary Bee Phase of Vespoid Type" upon them. Ferton's assertions concerning the transfer of the egg by the female wasp cannot be accepted. In the large number of *Ceramius* cells examined by me, the egg was left where it was first deposited and the larva upon hatching found its own way onto the nearby pollen loaf. There is no reason to suppose *C. tuberculifer* to be different in this



respect. Moreover, it is difficult to visualize how it would be physically possible for the female wasp to reposition her egg onto the pollen loaf, as the latter would be situated between her and the egg. It is therefore believed that Ferton drew incorrect conclusions and that Malyshev's hypothesis is therefore based on false premises.

Cell provisioning follows egg laying. The provision, unlike that of all non-masarine wasps but like that of most bees, is constituted of pollen and nectar. Pollen wasps transport the provision internally in the crop like the colletid bees of the subfamilies Euryglossinae and Hylaeinae but unlike the majority of bees which carry pollen loads for provisioning externally. Mass provisioning is the general rule (Chapter 5), although progressive provisioning has been alleged by Zucchi et al. (1976) for *Trimeria howardi* and by Brauns (1910) for *Ceramius lichtensteinii*. Brauns's contention was mentioned by Richards (1962), who did not comment other than to state that this was not recorded for the European species studied. Torchio (1970), presumably on the strength of Brauns's assertion, listed the genus *Ceramius* as practicing progressive provisioning in contrast to the genera *Gayella*, *Paragia*, *Pseudomasaris*, and *Celonites*, which he listed as not provisioning progressively. Malyshev (1968) not only accepted Brauns's statement but elaborated upon it, writing that "This method of progressive feeding of the larvae on honey [*sic!*], provided when it is needed and only given directly into the larva's mouth, is bound to reflect the moment . . . when the instincts of the wasp were transformed into those of the bee." We (Gess and Gess 1980), however, established that *C. lichtensteinii* practices mass provisioning, and, under optimal conditions of favorable weather and an abundance of forage flowers, provisioning and sealing of the cell is completed by the female before the egg hatches. Under less favorable conditions, the rate of provisioning is slowed down, leading to the finding of unsealed cells containing larvae and varying amounts of provision, and under really unfavorable conditions the situation as reported by Brauns results.

The egg phase, in common with all but the social wasps, lasts only a few days. Shortly before hatching the segmentation of the larva is visible through the pellicle.

The number of larval instars has not been recorded, however, five is the norm for aculeate wasps and bees. The only masarine larval descriptions are for the diapausing final instar larvae of *Pseudomasaris edwardsii* (Torchio 1970) and *Trimeria howardi* (Zucchi et al. 1976). Feeding is completed



during the final larval stage when the provision has all been consumed. The larva then commences spinning a cocoon closely attached to the walls of the cell so that it is inseparable from it except, in some at least such as *Ceramius*, at the truncate outer end. Characteristically of wasps, defecation occurs only once during larval development, that is following cocoon spinning. The larva then becomes semi-flaccid and markedly curved and enters a resting prepupal phase.

As in most solitary wasps and bees, it is the prepupa which overwinters. The prepupa enters a state of dormancy (diapause). Pupation and emergence as an adult may take place in the following spring or summer, but it is possible for diapause to last for some years.

As a general rule, at temperate latitudes pollen wasps appear to be univoltine. It is suggested by Zucchi et al. (1976), however, that *Trimeria howardi* in subtropical South America may be bivoltine.

The flight periods for pollen wasps, in the semi-arid areas of southern Africa at least, are variable according to the climatic conditions prevailing in a particular year. Certain generalizations may, however, be made. In the winter-rainfall area in the west, emergence is earlier than in the east, where the wettest seasons are spring and autumn. Thus emergences in the west start in August and peak activity can be expected in September/October. Thereafter, as the dry summer season advances and forage plant flowering is over and temporary pools of water dry up, there is a rapid falloff in activity. By December activity is over except in the vicinity of permanent water, where forage plant flowering periods are somewhat extended. In the east earliest emergences are in late September and greatest activity can be expected from early November to mid-December, depending on timing of rain. When rain has been late there has been a shift to December–January or January–February emergences. Late summer or early autumn rain has even resulted in a second but insignificant flush of nesting by *Jugurtia confusa* from February to early April (Gess and Gess 1980). In the north, in the southern Kalahari, where localized thunderstorms can be expected in late summer, coincident localized emergences of *Celonites* and *Quartinoides* and flowering of their forage plants are experienced (Gess and Gess 1991b).

A similar activity pattern appears to prevail in southern Australia, judging from the available records for *Paragia* (C.) *vespiformis* and *Paragia* (P.) *decipiens*. The former flies in the southwest from July until October (Houston 1986) whereas in the southeast the latter has been noted to be most

abundant in December (Naumann and Cardale 1987). Records from the middle and northern latitudes are too scanty to present a clear picture of activity patterns.

The few published collecting dates for *Trimeria* from South America are for the period November to May.

In the northern hemisphere collecting dates for the Mediterranean (Richards 1962) suggest that, in this winter-rainfall region, activity is in spring and early summer.

Collecting dates (Richards 1963b) for the North American masarine genus *Pseudomasaris* indicate a period of activity from March–April to July–August, depending on species, with the peak of activity being in April/May, June, or June/July, depending on species. Differences between climatic regions are not taken into account and are difficult to establish from the available data, however, the overall picture is emergence in early spring and peak activity in spring or early or mid-summer, according to species.

### *Mate location*

The evolution of insect mating systems has been explored in depth by Thornhill and Alcock (1983). They found that mate-location behavior appears to be evolutionarily labile, sensitive to and shaped by ecological pressures peculiar to a species. They stated that as a rule searching males tend to gather in that part of the environment where receptive females are concentrated but that males of species of which the females are scarce or widely scattered may employ the alternate strategy of waiting for females on landmarks.

Male masarines searching for females where they are concentrated can be predicted in all species to favor forage plant patches. For those species which use water in nest excavation and construction, water is an equally probable search location, as are nesting areas for species which nest in aggregations.

*Quartinia* and *Quartinoides* males rest on the ground in the vicinity of forage plants and rise up in response to the arrival of females, which they then mount and copulate with on the flowers (Gess and Gess 1992, and unpublished fieldnotes). *Celonites* males are similarly commonly present, apparently waiting, in the vicinity of forage plants (Gess and Gess 1992). On several occasions we have observed *Ceramius cerceriformis* males

perched on vegetation above a forage plant being visited by females but saw no interactions between them (Gess and Gess, fieldnotes). However, we have observed actual mounting of females by males on flowers by *Ceramius clypeatus* and *Ceramius lichtensteinii* (Gess and Gess 1990, and unpublished fieldnotes).

Males of *Rolandia angulata* have been observed by us patrolling plants on which females were foraging and grappling with females on the ground in close proximity to the plants (Gess et al. 1995).

Longair (1987) made observations on mating behavior at floral resources by two species of *Pseudomasaris*, *P. vespoides* and *P. zonalis*. These wasps patrolled patches of flowers where females obtained pollen and nectar for provisioning nests. Males patrolled several patches, but frequently remained within one patch for extended periods, perching and investigating insects which entered the patch. Absolute numbers of males were low, and while interactions between males were thus rare, they were sometimes intense. No size differences, based on head capsule width, could be distinguished between males that copulated ( $n = 13$ ) and males not observed to copulate ( $n = 60$ ).

*Paragia*, *Ceramius*, *Jugurtia*, and *Masarina* all use water in nest construction and males would therefore be able to contact females at water sources. Males of *Paragia* (*P.*) *decipiens* alight on water surfaces to drink in company with females. One record is given of a male attempting to mate with a female on the ground near water (Naumann and Cardale 1987). Males of 11 *Ceramius* species, *C. micheneri*, *C. toriger*, *C. braunsi*, *C. nigripennis*, *C. rex*, *C. metanotalis*, *C. lichtensteinii*, *C. bicolor*, *C. capicola*, *C. linearis*, and *C. socius*, have been observed by us at water (Gess and Gess 1980, 1986, 1988b, 1990, and unpublished fieldnotes).

Shortly after they emerge from their nests in the morning, female ground-nesting *C. socius* aggregate at a selected watering point. Fred and I have observed a hundred or more individuals congregating in this manner. The males join them and at this "swarming" point coupling takes place. A male having gained a firm hold on a female, the pair flies off together (Gess and Gess 1988b). On a fine day "swarming" continues until late afternoon. Although males are present abundantly with females at flowers and in nesting areas, we have not observed couplings in these locations.

We have frequently observed both sexes of *C. lichtensteinii*, *C. capicola*, and *C. linearis* flying up and down the length of a puddle together. The

females alight on the water surface, legs widespread. While a female is thus resting on the water surface and gently drifting, a male alights on top of her and both fly off together, the male grasping the female (Gess and Gess 1980). As noted above, *C. lichtensteinii* also couple on forage flowers. For this species, at least, coupling can take place in more than one location.

It is likely that *C. toriger* and *C. clypeatus* couple at water, as we have observed males of these species "waiting" in large numbers on raised ground at a short distance from and overlooking water being visited by females; however, no instances of pairing were observed (Gess and Gess 1990; D. W. Gess, unpublished fieldnotes).

Although we have observed large numbers of females of *Jugurtia confusa*, *Jugurtia braunsi*, and *Jugurtia braunsiella* collecting water from saturated soil at the water's edge, we have never seen males in attendance (Gess and Gess, unpublished fieldnotes).

Males of *Jugurtia confusa*, a ground-nesting species, appear in numbers shortly before the females and are present for most of the flight period, becoming scarce as the season advances. We have observed them flying low, 5–8 cm above the ground, particularly skirting bushes at the periphery of the nesting area and also alighting on the ground within the nesting area, where they sunned themselves and rose up to chase females and each other. They descended rapidly upon the females and although mating was not observed it seems likely that it takes place within the vicinity of the nesting area (Gess and Gess 1980).

Males of *Paragia* (*P.*) *tricolor* and *Paragia* (*P.*) *decipiens*, both ground-nesting species, are present in the nesting area. Houston (1984) noted that those of *P. (P.) tricolor* patrol the margins of the nesting area and observed a male pouncing on and grappling with a female. Those of *P. (P.) decipiens* have been seen to watch open nest entrances, but it was not noted whether they were waiting for females or guarding the nests (Naumann and Cardale 1987).

The male strategy of waiting for females on landmarks has been suggested for *Pseudomasaris maculifrons* (Alcock 1985). Males of this wasp perch on rocks in open areas on peaktops and ridges in central Arizona. The same areas are occupied from February to May in different years by different generations of males. Individuals regularly return to the same small perching location on a peaktop over an interval of as long as 29 days. As is the case with other "hilltopping" species, nesting and foraging females appear to be scarce and widely scattered.



### *Nest guarding*

We have observed males of six species of *Ceramius*, *C. micheneri*, *C. toriger*, *C. lichtensteinii*, *C. capicola*, *C. socius*, and *C. bicolor*, in association with nests (Gess and Gess 1980, 1986, 1988b, 1990).

*C. socius* males are present in the nesting areas before the females emerge from their nests in the morning. After pairing with the females at their watering point they do not, however, seem to return to the nesting area, and no males were found sheltering in nests (Gess and Gess 1988b). On the other hand, male *C. bicolor* guard the nests while the females are away from them (Gess and Gess 1986). Each nest seems to be attended by a male. The male guard drives off other males or any other insects that come too near the nest. On a cloudy day, when I investigated four nests, two contained a male each. These two nests each contained an unsealed but provisioned cell. Males of *C. lichtensteinii* and *C. capicola* similarly are present in the nesting area while nesting activities are in progress (Gess and Gess 1980). I have noted one instance of a male *C. micheneri* and two of a male *C. toriger* together with a female in her nest (Gess and Gess 1990).

Zucchi et al. (1976) found males and more than one female in nests of *T. howardi* but did not apparently observe nest-guarding behavior.

### *Sleeping and sheltering*

When nests are being worked upon, sleeping or sheltering in the nest by females at night or in inclement weather seems to be common among the pollen wasps. These behaviors have been recorded for *Ceramius capicola*, *C. socius*, *C. lichtensteinii*, *C. toriger*, *C. nigripennis*, *C. micheneri*, *Jugurtia confusa*, *Celonites latitarsis* (Gess and Gess 1980, 1986, 1988b, 1992), and *Pseudomasaris edwardsii* (Torchio 1970).

As aerial nesters do not have burrows, the nest is available for sheltering only when there is an open cell. When there is no open cell, an alternative sleeping place must be found. *Celonites abbreviatus* has been observed sleeping rolled around a grass culm, with the antennae folded downward, the retracted legs pressed into their resting position on the thorax, and the folded wings clamped in the gap between the thorax and the abdomen (Bischoff 1927). There is a single record of a female *Celonites andrei* sleeping on a dry stem on to which it was holding with its mandibles

(Brauns 1905). Females of *Pseudomasaris edwardsii* have been recorded sleeping within the corolla tube of the forage plant flower, *Phacelia* sp., and exposed clinging to green seed pods of mustard, *Brassica* sp. (Torchio 1970).

As already indicated in the section on nest-guarding behavior, the males of some species of *Ceramius* are known to shelter and sleep in nests with or without females. Male *Masarina mixta* commonly sleep in the flowers of *Wahlenbergia* to which they and the females come to forage (Gess and Gess, unpublished fieldnotes). No females have been found sleeping in the flowers and it seems most likely that they sleep in their nests, which are most probably burrows.

There are no records of sleeping aggregations.

### *Evolutionary considerations*

That pollen wasps are, as far as is known, essentially solitary wasps is perhaps not surprising when it is considered that they are principally wasps of semi-arid areas outside the tropics (Chapter 2). The development of sociality and a tendency to sociality among wasps, as with insects in general (Wilson 1979) and with bees in particular (Roubik 1989), is principally associated with humid subtropical to tropical areas. Little is known of nesting by those few pollen wasps which do occur in the tropics. If development toward sociality does occur in the masarines, it is most probable that it is among these that it will be found.

Some of the behavioral characters considered to be prerequisites for the evolution of eusociality are present. Oviposition into an empty cell has been thought to be important in permitting the evolution of the extended brood care characteristic of social wasps (Evans 1957). The possibility of nest sharing, the basis of West-Eberhard's model for the evolution of sociality, (1978) is suggested. Carpenter (1991) considers cell reuse to be an important character. This is most certainly not uncommon in the masarines (see Chapter 5). Progressive provisioning and brood care, though shown to have been mistakenly attributed to *Ceramius lichtensteinii* by Maleshev (1968), could be evolved from delayed provisioning and is suggested for *T. howardi*. The short adult phase and long prepupal phase characteristic of the species living in semi-arid areas with seasonal rain, however, preclude a continuous chain of interaction between adults of different generations required for eusociality. It is conceivable that some



masarines in the tropics might be living under conditions conducive to a proportional change.

Evans and Eberhard (1970) gave a brief summary of what they understood to be the evolution of the nesting behavior of solitary wasps. They presented this as a series of ten steps, a "social ladder." The simplest step in the extant Vespidae, labeled Nest-egg-(prey)<sup>n</sup>-[cell closed & new cell prepared-egg-(prey)<sup>n</sup>]<sup>n</sup> and ranked "step 7b," is shared by the Euparagiinae and Eumeninae. If "provision load" is substituted for "prey" then the Masarinae also share this step. If one considers the position of the bees on this ladder, again substituting "provision load" for "prey," then the lowest step represented is "step 5c," Nest-(prey)<sup>n</sup>-egg-closure. Following Evans and Eberhard, the masarines must be considered to be at a higher step on the evolutionary ladder toward sociality than the vast majority of solitary bees.

In his consideration of the "genesis of the bees," Malyshev (1968) sought to find among the masarines, whose evolution he saw as parallel to that of the bees, a clue to the possible way in which the change took place from provisioning with arthropods to provisioning with pollen and nectar. He thus saw the change as being loss of provision with prey and instead direct feeding of the larva with "honey food," which being "juicy" could not be prepared in large amounts in the cells. He considered that later, "when appropriate adaptations had taken place in the mother wasp and, in particular, in her mouthparts, directed towards collecting flower pollen, she began to feed her larvae on a thicker and more concentrated food, containing an abundance of protein-rich pollen." This he saw as leading to the abandonment of progressive provisioning in favor of mass provisioning with a pollen loaf. This theory breaks down at the outset as his first phase was based on his mistaken belief that *Ceramius lichtensteinii* larvae are fed directly with "honey." It does not seem that the masarines will provide the answer to how the change could have taken place from provisioning with arthropods to provisioning with pollen and nectar.

Categories of nesting behavior (levels of sociality), modified from Wilson (1971), Michener (1974), and Eickwort (1981), found among Vespidae are set out by Cowan (1991). Following this scheme—in which there are three main categories, solitary, presocial, and eusocial—*Trimeria howardi* has been classed as presocial, as it exhibits social behavior beyond sexual interactions, more than one female having been found together in a nest in 12 out of 30 nests investigated. Zucchi et al. (1976), on the basis of their

own findings and following Michener (1974), tentatively interpreted its nesting as communal, but stated that some nests suggest quasisociality. Following Cowan's definitions, if it is found that each female builds, oviposits in, and provisions her own cells, communal nesting will be confirmed, but if it is found that all females cooperate in building and provisioning brood cells and all females oviposit, then quasisocial nesting will be confirmed. Further evidence is needed to take the classification this far. Nevertheless, however far it may be found that pollen wasps in the tropics have evolved toward sociality, the fact will remain that evolution to sociality in the social vespids did not stem from the masarines. Any advance toward sociality in the masarines evolved separately.

# Nesting

In this chapter the available species nesting accounts for the pollen wasps of the world are assembled and synthesized to give generic accounts. Under each genus published records are initially referred to by author. To avoid continuous repetition authors are not cited throughout. The accounts are presented in a consistent form under the headings: nesting areas and nest situation; provision; water collection; description of the nests; method of construction of the nest; and reuse of nests. The taxa are ordered as in Table 2. There follows a discussion of nesting under the headings: basic nest types, bonding agent, method of excavation, evolutionary sequence, and oviposition and provisioning.

## *Nesting accounts*

### Gayellini

#### *Gayella* Spinola

There appears to be only one published record of the nesting of the Neotropical genus *Gayella*, that for *G. eumenoides* (Claude-Joseph 1930), which constructs aerial nests.

#### NEST SITUATION

The nests are attached to rocks.

## PROVISION

The pollen and nectar provision must be very moist, as it was suggested by Claude-Joseph that nectar alone is stored.

## DESCRIPTION OF THE NEST

The nest consists of constructed mud cells attached in groups to rocks. The cells are shortly ovoid and arranged side by side in a line. Sometimes up to three such rows of cells may be parallel to and touching one another. The groups of cells are normally partly obscured by a layer of mud.

## REUSE OF NESTS

Old cells may be cleaned out and used again.

### *Paramasaris* Cameron

There appear to be no records of nesting by *Paramasaris*.

## Masarini: Paragiina

### *Paragia* Shuckard

Nesting has been recorded for four species of the Australian genus *Paragia*: three species of *Paragia* (*Paragia*), *P. (P.) smithii* (Wilson 1869; observations only of females coming and going from turreted burrows), *P. (P.) tricolor* (Houston 1984), *P. (P.) decipiens* (Naumann and Cardale 1987); and one species of *Paragia* (*Cygnea*), *P. (C.) vespiformis* (Houston 1986). All excavate a vertical to subvertical burrow in the ground. No nests of *Paragia* (*Paragiella*) have been recorded.

## NESTING AREAS AND NEST SITUATION

From a comparison between vegetation maps for Australia (Groves 1981) and the distribution map for masarines (Fig. 5) it would appear that paragiines are most commonly associated with somewhat open *Eucalyptus*

woodland or shrubland, vegetation generally higher than that of most of the semi-arid areas of the world, although equally sparse.

*Paragia* (*P.*) *tricolor* and *P. (P.) decipiens* were recorded as nesting in clayey soil in close proximity to water and *Eucalyptus* (Myrtaceae) woodland (Houston 1984, Fig. 1), *E. calophylla* and *E. camaldulensis* respectively. No description of the nesting area of *P. (P.) smithii* was given.

*Paragia* (*C.*) *vespiformis* was recorded as nesting in sandy soil between dunes in *Acacia* (Mimosaceae) and *Grevillea* (Proteaceae) scrub.

#### PROVISION

The provision, a pollen and nectar mixture, is in the form of a loaf having folds and annulations and increasing in diameter toward the open end of the cell. That of *P. (C.) vespiformis* rests on papillae (Houston 1986, Fig. 6).

The pollen loaves of *P. (P.) tricolor* and *P. (P.) decipiens* were each constituted of a single pollen type matching pollen of *Eucalyptus calophylla* and *Eucalyptus camaldulensis* respectively. Those of *P. (C.) vespiformis* were constituted of *Acacia* pollen.

#### WATER COLLECTION

Water collection by the three species of *Paragia* (*Paragia*) and *P. (C.) vespiformis* was recorded. Furthermore it was noted that *P. (P.) decipiens*, *P. (P.) smithii*, *P. (Paragiella) odyneroides*, and *P. (C.) vespiformis* alight on the water surface.

#### DESCRIPTION OF THE NESTS

In all instances the burrow is subvertical. That of *P. (P.) smithii* and *P. (P.) tricolor* is surmounted with a vertical or curved to horizontally opening mud turret. That of *P. (P.) decipiens* allegedly lacks a turret, but it is stated that where entrances were concealed beneath leaves or rocks, the shaft was extended above ground level as an incomplete thin-walled tube. The burrow of *P. (C.) vespiformis* lacks a turret.

The subterranean nest structure of *P. (P.) smithii* was not recorded. The nests of *P. (P.) tricolor* (Figs. 22a,b) and *P. (P.) vespiformis* (Figs. 22d,e) are multicellular, nests with up to 14 cells and four cells respectively having

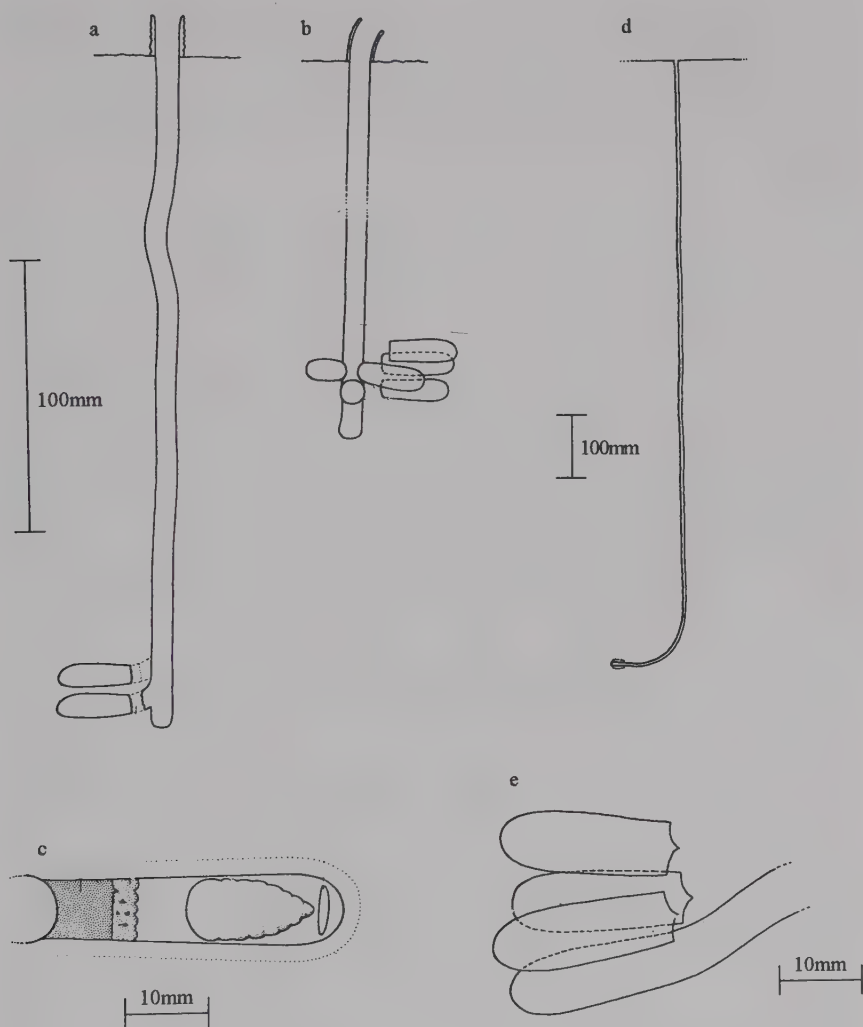


Figure 22. Vertical plans of turrets and underground workings of nests of *Paragia* species: (a-c) *P. (P.) tricolor* (from Houston 1984), no cell terminating main shaft; (d and e) *P. (C.) vespiformis* (from Houston 1986), cell terminating main shaft.



been recorded. Only one nest of *P. (P.) decipiens* had a cell; however, it is likely that the nest of this species is also multicellular.

The cells consist of an excavated cell within which is a constructed mud cell. The inner surface of the cell of *P. (P.) tricolor* is polished and waterproofed.

#### METHOD OF CONSTRUCTION OF THE NEST

The turret of *P. (P.) tricolor* is constructed in the initial stages of burrow excavation. It is smoothed on the inner surface. Pellets not used in turret construction are carried away from the nest and discarded. The main shaft is excavated in such a way that its diameter equals the inner diameter of the turret and this diameter is maintained constant throughout its length. While excavating the shaft the wasp always reverses out of the burrow, indicating that it cannot turn within the shaft as do species of *Ceramius* which construct a turning "bulb." The diameter of the main shaft of the nests of *P. (P.) decipiens* and *P. (C.) vespiformis* is similarly constant throughout.

No cell terminates the main shafts of the two *Paragia (Paragia)* species. Short horizontal lateral shafts each terminating in a cell are excavated, usually all to one side of the shaft. In the nest of the *Paragia (Cygnea)* species, *P. (C.) vespiformis*, the main shaft curves at its lower end to terminate in a horizontal cell. Further cells terminate secondary shafts, all of which are excavated to one side of the main shaft.

The cells attained their maximum diameters near their rounded ends. Recorded wall thicknesses are about 2 mm (*tricolor*), 1–2 mm (*decipiens*), and 0.5 mm (*vespiformis*). It was not established whether the constructed mud cells were built in or formed by impregnation of the walls of the excavated cavities, nor what was the nature of the substance used for polishing and waterproofing them.

Following oviposition and provisioning, each cell is closed with a plug of cemented earth, followed by compacted soil filling the access burrow, which is then sealed off flush with the main shaft.

#### *Riekia* Richards

Little has been recorded concerning the nesting of *Riekia*. An undescribed species of *Riekia* was observed entering burrows in sandy ground (Houston

1984). The burrows were simple, oblique, and ended blindly without any cells, and neither had an entrance turret.

#### PROVISION

The two species of *Riekia* for which flower visiting has been recorded were visiting flowers solely of Goodeniaceae (Appendix 1), suggesting that nectar and pollen for provision are obtained from plants of this family.

#### WATER COLLECTION

*Riekia nocatunga* in open *Eucalyptus* woodland at Southwood in Queensland and *Riekia confluens* in open scrub near Carnarvon in Western Australia were observed alighting on water (Gess, Gess, and Gess, unpublished fieldnotes, October 1993), which suggests that some species at least may use water in nest excavation and construction. That the soil in these areas had a high enough clay factor to be malleable when mixed with water was established by the presence of species of pompilids and eumenines, which we observed using water in nest excavation and construction.

#### *Rolandia* Richards

Nesting by two species of *Rolandia*, *R. angulata* (Gess et al. 1995) and *R. maculata* (Houston, pers. comm., February 1993), has been recorded.

#### NESTING AREAS AND NEST SITUATION

We located two nesting areas of *Rolandia angulata* between St. George and Cunnamulla in southern Queensland, one in dry open woodland dominated by *Eucalyptus* and the other in dry open scrub dominated by *Acacia*. Both areas had recently received rain in the form of localized thunder-showers, which had resulted in there being a growth of annuals in flower on the road verges and in the low-lying areas. The soil in both areas is sandy, compact but friable. It was increasingly moist at least to the depth of the deepest nest cells. The nests were situated at the base of a plantlet, pebble, or suitable item of debris.

The nesting area of *R. maculata* discovered by Houston was a sandy firebreak in Kings Park, Perth, Western Australia.

#### PROVISION

Provision was obtained from three cells of *R. angulata*. Each was a firm, white pollen loaf. The pollen was examined microscopically and found to match that obtained from flowers of *Goodenia* species.

#### WATER COLLECTION

No species of *Rolandia* have been recorded at water.

#### DESCRIPTION OF THE NEST

The nest of *R. angulata* consists of a subterranean burrow excavated in horizontal sandy soil (Fig. 23). The entrance is a simple hole, not surmounted by a superstructure. The burrow slopes gently downward for a short distance, after which it descends vertically (the diameter narrowing after approximately 80 mm) until it curves outward subhorizontally and ends in a cell which is rounded at the inner end. The cell is not lined in any way. Successive cells terminate similarly outwardly curved burrows radiating out through 360° from the vertical burrow, each deeper than that preceding it. The lateral burrows from the cell to the vertical shaft are, after oviposition and provisioning has been completed, packed with sand. Up to seven cells per nest were recorded.

The nest of *R. maculata* consists similarly of a vertical, unlined burrow with unlined cells at its lower end.

#### METHOD OF CONSTRUCTION OF THE NEST

Water is not required for the excavation of the nest as the sandy soil, though compact, is friable. In both species the sand extracted from the burrow is carried out of the shaft held between the underside of the head and the prosternum, the genae being fringed with stiff hairs (Snelling's "ammochaetae").

During the initial stages of burrow excavation *R. angulata* was observed to drop the extracted sand in a more or less constant area to one side of

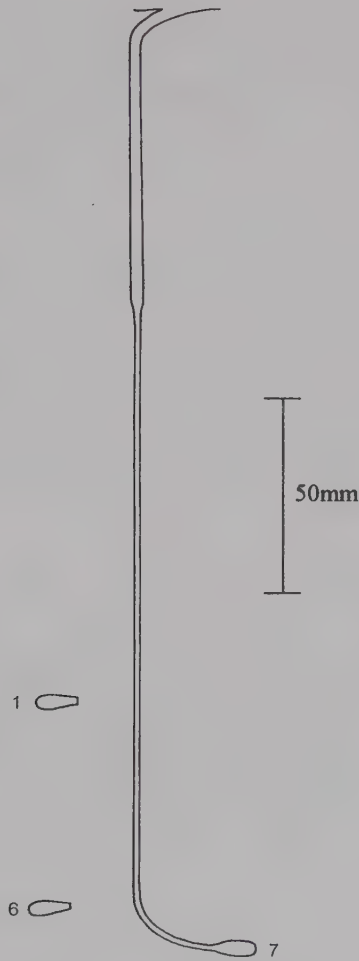


Figure 23. Plan of vertical section of a nest of *Rolandia angulata*. Cells 2-5 followed cell 1, radiating out in sequence through 360°.

the entrance and about 120 mm from it. As the burrows became deeper the extracted sand was dropped further from the nest in a constant arc about 250 mm from the entrance. The sand being scattered, there was no detectable accumulation and so no tumulus developed.

The sand used for packing a shaft leading to a cell is almost certainly obtained within the nest from the excavation of the shaft leading to the next cell.

*Metaparagia* Meade-Waldo and *Ammoparagia* Snelling

There appear to be no records of nesting by *Metaparagia* and *Ammoparagia*.

## Masarini: Masarina

*Ceramius* Latreille

Nesting has been recorded for three Palaearctic species of *Ceramius*:

Group 1, *C. fonscolombei* (incomplete nest, Fonscolombe 1835);

Group 7, *C. tuberculifer* (Giraud 1871; Ferton 1901) and *C. bischoffi* (incomplete nest, Richards 1963a)

and for fifteen Afrotropical species of *Ceramius*:

Group 2A, *C. cerceriformis* (Gess and Gess 1988b);

Group 2B, *C. clypeatus* (Gess and Gess 1990);

Group uncertain, probably 2B, *C. micheneri* (Gess and Gess 1990);

Group 3, *C. nigripennis* (Gess and Gess 1986), *C. jacoti* (Gess and Gess 1988b), *C. braunsi* and *C. toriger* (Gess and Gess 1990);

Group 4, *C. beyeri* (incomplete nest, Brauns 1910; incomplete nest, Gess and Gess 1988b);

Group 5, *C. lichtensteinii* (Brauns 1910; Gess and Gess 1980);

Group 6, *C. rex* (Gess and Gess 1988b) and *C. metanotalis* (Gess and Gess, unpublished fieldnotes);

Group 8, all four species, *C. capicola* and *C. linearis* (Gess and Gess 1980), *C. bicolor* (Gess and Gess 1986) and *C. socius* (Gess and Gess 1988b).

All excavate a vertical to sub-vertical burrow in the ground.

## NESTING AREAS AND NEST SITUATION

In southern Africa *Ceramius* species nest in areas of dry fynbos or karroid scrub (Fig. 8, Plates 1–8; Gess and Gess 1986, Figs. 1, 4, 5, 6, 20; 1988,

Figs. 1, 2, 3; 1990, Figs. 1, 5, 7) in relatively close proximity to their forage plants and a water source. *Ceramius* appears to show a preference for horizontally presented soil though some species, *C. lichtensteinii*, *C. jacoti*, *C. braunsi*, and *C. socius* at least, will nest in sloping ground. *Ceramius* species have never been found nesting in vertically presented soil.

The soil particle size varies from relatively coarse to very fine. In all instances the clay factor is sufficient that the soil is malleable when mixed with water. Nests are aggregated in bare areas. Nest aggregation siting varies from apparently random within a bare area to a definite positioning. Several different nesting sites need to be visited before a definite positioning can be assumed. The nests of *C. nigripennis* always seem to be in close proximity to the base of a bush, whereas those of *C. socius* may be fully exposed and massed in the center of a large bare area or scattered in bare areas between the spreading branches of its forage plant.

#### PROVISION

The provision, a pollen and nectar mixture, is in the form of a firm pollen loaf positioned at the blind end of the cell, free from the cell walls and filling the cell to about two thirds of its length (Fig. 29). I examined microscopically pollen from the provision of all species investigated by us and compared it with the pollen of flowers found in the vicinity of the nesting area. For each species I found that the provision was derived from flowers of a single family or genus and furthermore that this was constant within a species group. This finding is supported where we obtained only foraging records. Furthermore, foraging records indicate that nectar is almost always derived from the same flowers as is pollen. *Ceramius* species/forage plant associations are given in Table 6.

#### WATER COLLECTION

The nearness of nesting sites to a water source is either stated or implied by all authors and all the species are recorded as visiting water. Fred and I have shown that all species studied fill the crop with water, which, when regurgitated upon the clayey nesting substrate, makes the latter more easily worked and thus makes nest construction possible. Similarly, Ferton (1901) with respect to the pool visiting of *C. tuberculifer* made it abundantly clear that what the wasp collects is water, not mud.



Other authors, however, have claimed that some species, at least, collect not water but mud. Fonscolombe (1835) stated that *C. fonscolombei* went to ponds to collect sodden earth ("terre délayée"). Later in his account, though, he appears to have been uncertain for he stated that the turret was constructed of pellets derived from the excavation of the nest (which would indicate the collection of water, not mud) or of pellets carried to the nest from without (which would support his earlier contention).

Similarly, Brauns (1910) stated that whereas *C. beyeri*, *C. lichtensteinii*, and *C. linearis* settle on the water surface at the middle of the pool to collect water, *C. cerceriformis*, *C. bicolor*, and *C. capicola* alight at the edge of the pool and collect mud in little pellets, which he maintained are used by them for the construction of their cells and turrets. However, we have shown Brauns to have been mistaken. Those species which alight at the edge of the pool do not collect mud but, like those which alight on the water surface, collect water.

It seems that water-collecting behavior is most usually constant for species and species groups.

All four species of Group 3, *C. nigripennis*, *C. jacoti*, *C. braunsi*, and *C. toriger*, the single species of Group 5, *C. lichtensteinii*, and two species of Group 6, *C. rex* and *C. metanotalis* (water collection has not been observed for the third species, *C. caffer*) alight on the water surface to collect water (Plate 9).

Three species of Group 2, *C. cerceriformis*, *C. clypeatus*, and *C. richardsi* (water collection has not been observed for the fourth species, *C. peringueyi*), and *C. micheneri* (group uncertain) alight at the edge of the water.

Group 8 seems to be exceptional in showing intra- and interspecific variation in water-collecting behavior. *C. linearis* alights on the water surface, *C. bicolor* and *C. socius* collect water from the damp soil at the water's edge (Plate 10), and *C. capicola* seems to collect water either on the water surface or at the water's edge.

#### DESCRIPTION OF THE NESTS

All the known nests of *Ceramius* species consist of a multicellular subterranean burrow surmounted by a subvertical or curved tubular mud turret (Plate 11, Figs. 24–26) of the same diameter as the burrow opening. Each successive cell terminates a secondary shaft. The section of the secondary shaft between the cell and the main shaft is filled with soil and is sealed



Figure 24. *Ceramius capicola* female building nest entrance turret.



Figure 25. Nest entrance turret of *C. jacoti*.



Figure 26. Nest entrance turret of *Ceramius metanotalis*. Note discarded mud pellets.

off from the main shaft with a thin mud plate. Within each excavated cell of all but Group 8 is a constructed mud cell sealed with a mud plug (Figs. 27–29). The diameter of the cells is greatest toward the rounded end. The structure of the subterranean burrow differs between species groups but is constant within a group.

For Group 1 nesting has been recorded for only one of the three species. No details of the subterranean burrow are given.

In the nests of Group 2A and B (Figs. 30a and c) the relatively long, slender main shaft descends subvertically and for the greater part of its length is of the same diameter as the burrow entrance. Near the lower end of the shaft there is a short wider section forming a “bulb,” below which the shaft continues with a diameter equalling that of the upper section of the shaft. The main shaft at its base turns outward to form a short lateral shaft terminating in a cell which lies subhorizontally. Successive cells terminate secondary lateral shafts and all lie to one side of the shaft in a group. The nests of *Ceramius micheneri* (Fig. 30b) investigated were all at the first cell stage and at that stage they resemble those of Group 2.

In the nests of Group 3 (Fig. 31) the burrow consists of a short shaft, having the upper part of the same diameter as the entrance and the lower part of a diameter up to three times as great, depending upon the number of cells present. From the basal “bulb” extend very short, subvertical secondary shafts, each terminating in a cell.

The nature of the nests of Group 4 is incompletely known. Burrows of *C. beyeri* investigated by both Brauns and myself were incomplete and those of *C. damarinus* are unknown.

In the nest of the monospecific Group 5 (Fig. 32) the relatively long main shaft descends subvertically. For the first third of its length it is of the same diameter as the burrow entrance. There follows a short wider section forming a “bulb,” below which the shaft continues with a diameter equalling that of the upper section of the shaft. No cell terminates the main shaft. Extremely short, horizontal, lateral, secondary shafts roughly grouped in whorls radiate out from the main shaft at depths from shortly below the “bulb” to a short distance above the base of main shaft.

In the nests of Group 6 (Fig. 33), characterized on the basis of the nesting of two of the three species, the main shaft is of moderate length, descends subvertically, and is initially of the same diameter as the entrance





Figure 27. Vertical cutaway of newly constructed one-celled nest of *Ceramius jacoti*, showing bulb and constructed earthen cell.



Figure 28. Constructed earthen cells of *Ceramius nigripennis*: half-constructed (top left) and completed and sealed (top right), and group of four (bottom).

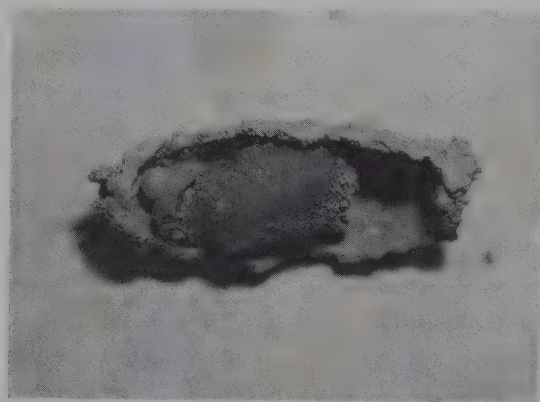


Figure 29. Constructed earthen cell of *C. cerceriformis*, cut longitudinally to show provision and position of young feeding larva.

but widens after some distance. The wider section of the main shaft varies in length from nest to nest. In some new nests with only one cell the wide section is no more than a "bulb" below which the shaft continues with a diameter equalling that of the upper section of the shaft. In nests at a more advanced stage, that is, with several cells, the entire lower section of the subvertical shaft is wide. In some nests the diameter of this lower wide section of the shaft fluctuates so that its sides are very uneven. At the base of the subvertical section the shaft curves outward to terminate in a cell which lies subhorizontally. Subhorizontal secondary shafts, each terminating in a cell, fan out from the main shaft but never form a complete whorl so that the cells lie together in a group. In some instances the cells are at different depths but always forming a group.

For Group 7 nesting has been recorded for only one of the six species. No details are given of the general nest plan, but it is recorded that a mud cell is constructed within an excavated cell.

In the nests of Group 8 (Fig. 34), based on all four species, the relatively long main shaft descends subvertically and is of the same diameter as the entrance with, usually, at approximately half its depth a short "bulb." Toward its lower end the main shaft curves to one side and terminates in a sloping cell. Relatively long secondary shafts diverge from the main shaft at the level at which it departs from the subvertical. Each secondary shaft ends in a cell. An excavated cell is smoothed on the inside. Mud cells are not constructed. A completed cell is sealed with a mud plate.

## METHOD OF CONSTRUCTION OF THE NEST

Nest excavation is initiated by the female's regurgitating water from her crop onto the ground. Using her mandibles, she works this water into the earth to form mud from which she forms a pellet. A number of pellets are formed in this way from a cropfull of water. The first pellets excavated from the shaft-initial may be discarded. The shaft-initial is circular in cross

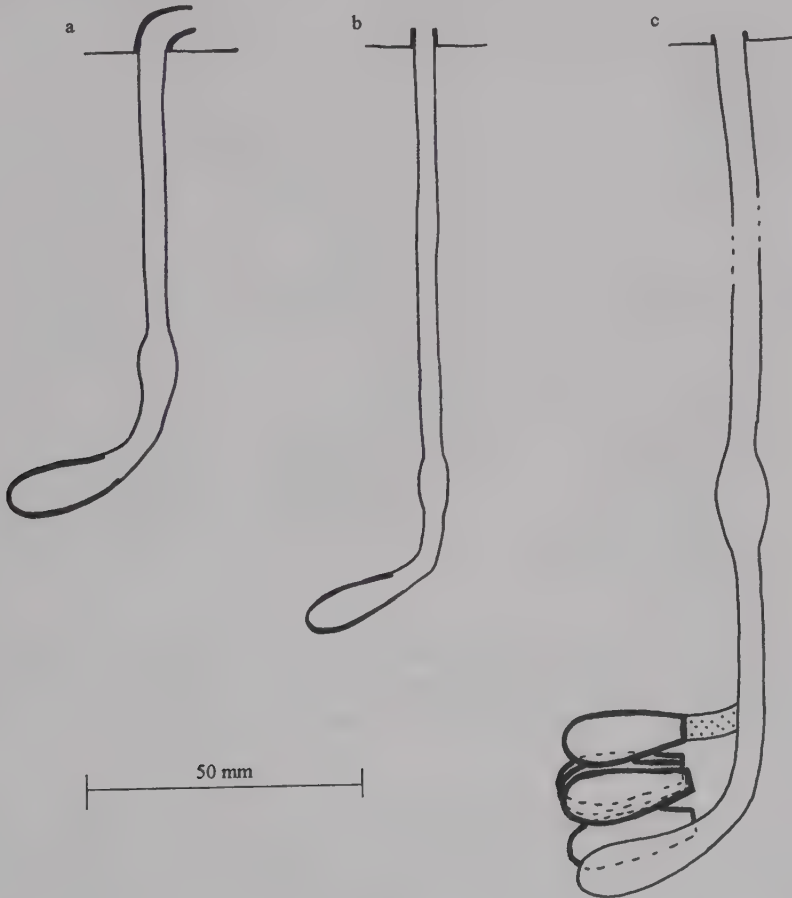


Figure 30. Vertical plans of nests of *Ceramius* Group 2 and of the closely allied *Ceramius micheneri*: (a) *C. cerceriformis*; (b) *C. micheneri*; (c) *C. chyeatus*. Nests are characterized by cells terminating main shaft, cells subhorizontal and grouped to one side of main shaft, and constructed cells within excavated cells.



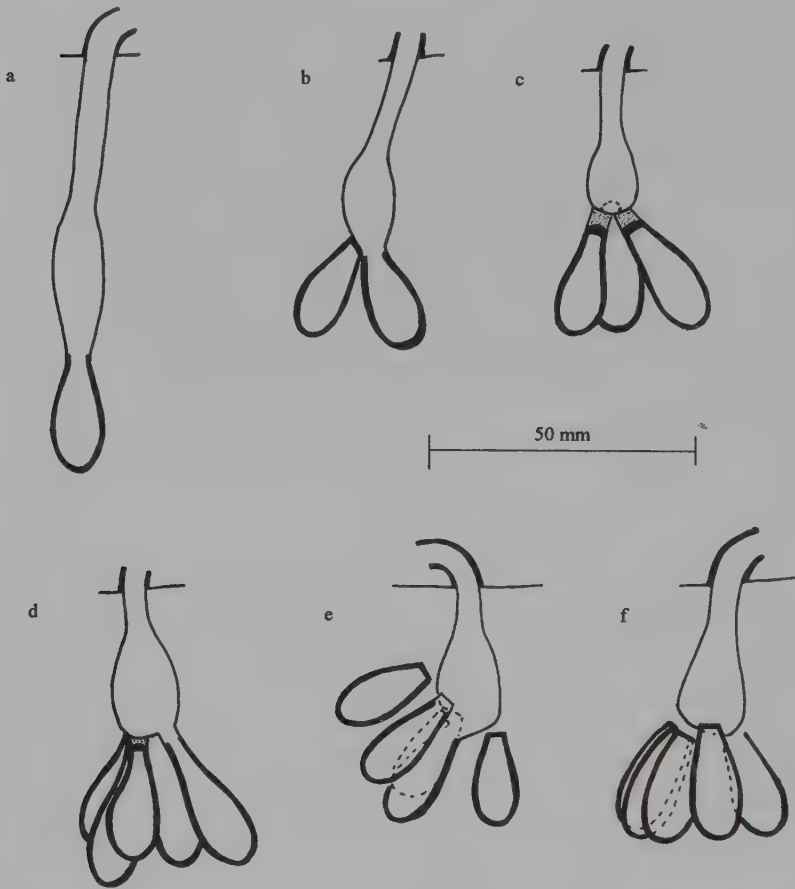


Figure 31. Vertical plans of nests of *Ceramius* Group 3: (a) *C. jacoti*; (b–d) *C. nigripennis*; (e) *C. toriger*; (f) *C. braunsi*. Nests are characterized by cells terminating main shaft, cells subvertical, grouped beneath the basal “bulb,” and constructed cells within excavated cells.

section as a result of the female’s rotating evenly and always completing a circle. At the commencement of turret construction, the pellets, instead of being discarded, are laid down in a circle around the shaft-initial in such a way that the inner diameter of the turret will be the same as that of the shaft.

Shaft diameter is in almost direct proportion to head width. Thus head width (measured across the eyes) ranges from 2.5–2.8 mm (*bicolor*) to 4.6–5.3 mm (*rex*) and shaft diameters range from 3.5–4.0 mm (*bicolor*) to

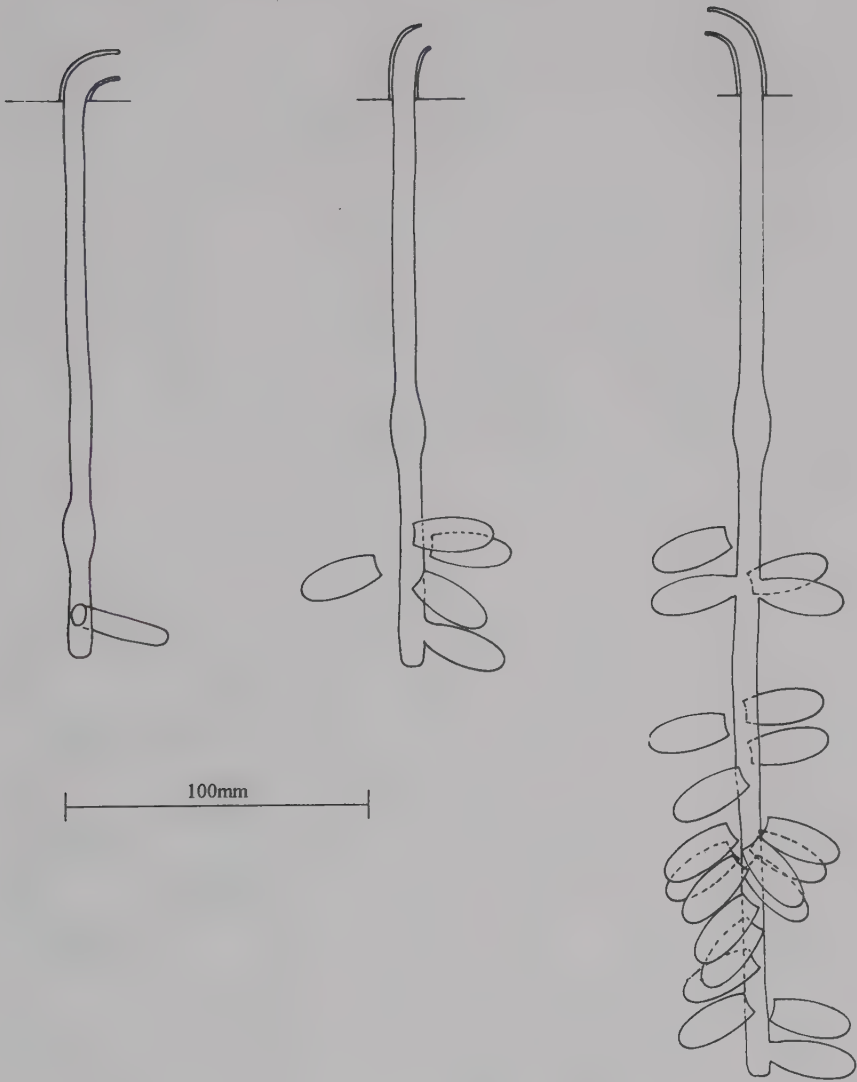


Figure 32. Vertical plans of nests of *Ceramius* Group 5: *C. lichtensteinii*. Nests are characterized by lack of cell terminating main shaft, cells horizontal, not grouped to one side of shaft, and constructed cells within excavated cells.

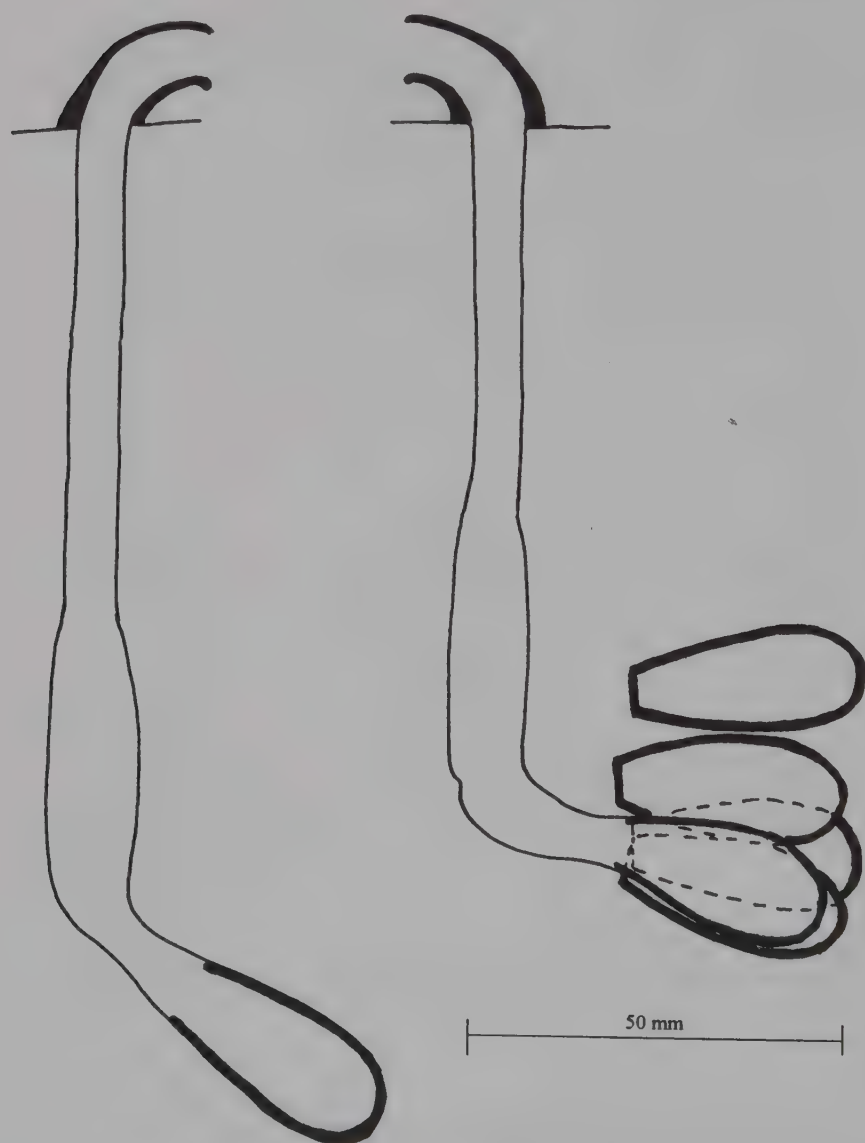


Figure 33. Vertical plans of nests of *Ceramius* Group 6: *C. rex*. Nests are characterized by cell terminating main shaft, cells subhorizontal and grouped to one side of main shaft, and constructed cells within excavated cells.

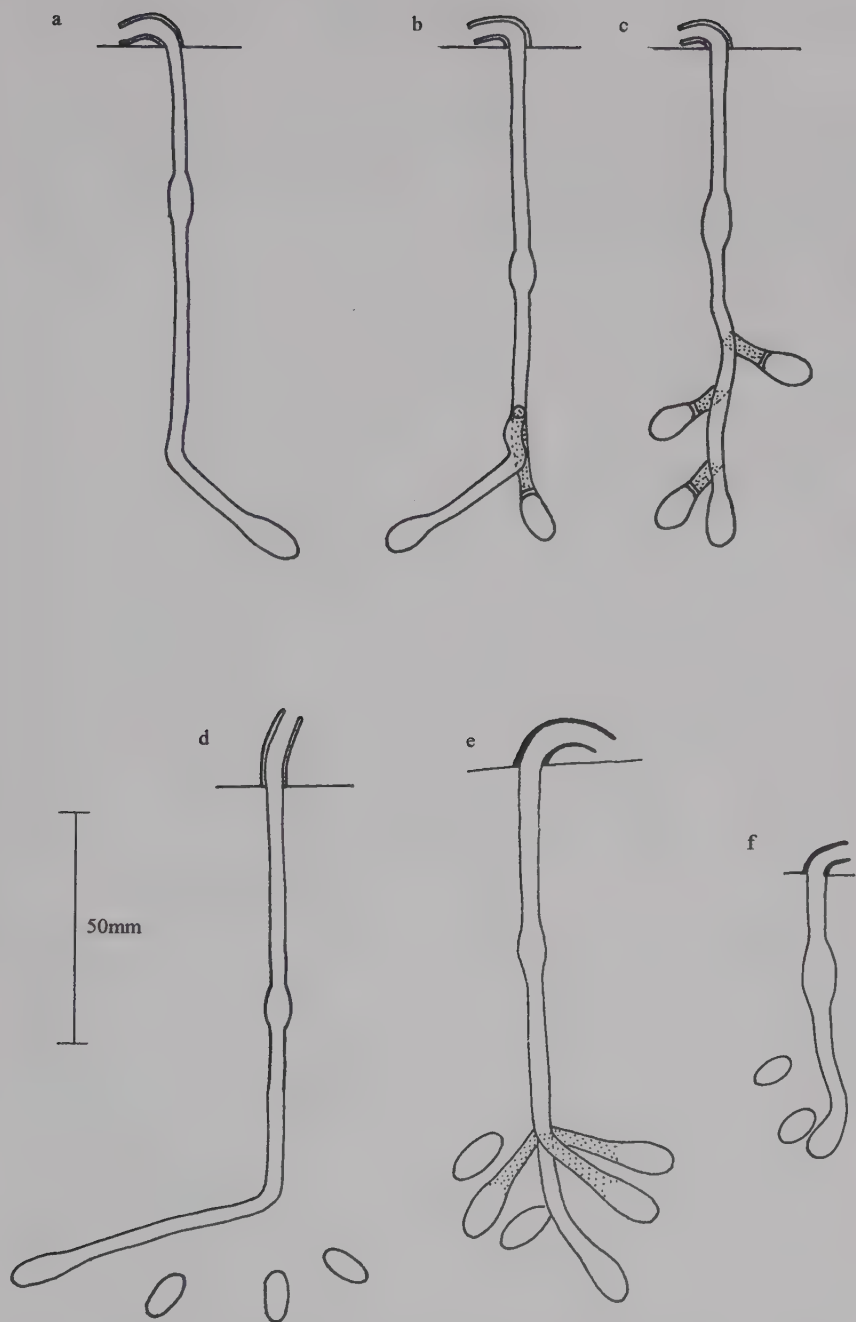


Figure 34. Vertical plans of nests of *Ceramius* Group 8: (a–c) *C. capicola*; (d) *C. linearis*; (e) *C. socius*; (f) *C. bicolor*. Nests are characterized by cell terminating main shaft, cells sloping, not grouped to one side of main shaft, and no constructed cells within excavated cells.

5.5–7.0 mm (*rex*). The variation in shaft diameter within a species is similarly explained by the variation in head width in individuals. This is nicely illustrated by my finding that nesting *C. lichtensteinii* at Hilton in the eastern Karoo had an average female head width (measured across the eyes) of 5.03 mm ( $n = 30$ , range 5.0–5.5 mm) and average shaft diameter of 6.2 mm ( $n = 19$ ), whereas at Tierberg in the southern Great Karoo, where average female head width was 6.35 mm ( $n = 30$ , range 6.0–7.0 mm), shaft diameter was 8.0 mm ( $n = 22$ ). In other words the head width of the Tierberg population was 26 percent greater than that of the Hilton population and shaft diameter was 29 percent greater.

Fred and I observed the method of placement of pellets by *C. capicola* most clearly. The wasp backs up the shaft with a pellet between her mandibles and, reaching the turret opening, holds the sides of the turret with her legs while placing the pellet in position and smoothing it on the inner surface with her mouthparts and supporting it on the outer surface with the tip of the ventral surface of her abdomen, which is curved around for this purpose (Fig. 24). As many as twelve pellets may be added to the turret per water load. If the turret is destroyed by rain or mechanical means, the wasp will build a new one of similar design and dimensions as the original one.

In the construction of a vertical cylindrical turret pellets are added regularly, whereas in a sloping or curved turret more pellets are added to that part of the turret wall which will be uppermost than to that which will be lowermost.

The turret having been completed, the wasp continues to excavate the shaft, but the pellets then extracted are discarded either in a definite pellet-dropping area in close proximity to the nest (Fig. 26) or at some distance. *C. capicola* is an example of a species which has a clearly defined pellet-dropping area. When discarding a pellet, a female of this species backs out from her nest until her head is free from her turret, then flies sideways and slightly forward just above the surface of the ground to the pellet-dropping area a few centimeters from and to one side of the turret. She drops the pellet and, still orientated parallel to her turret, flies in reverse motion back to the nest entrance, which she is then facing, and enters (Fig. 35). In this way the pellet-dropping operation takes up the minimum of time and exertion, differing from that of most mud-excavating wasps, including some species of *Ceramius* that fly up in a wide circle when dropping pellets. In some species whether or not pellets are dropped in close proximity to nests or at some distance varies between populations, both behavior patterns having been ob-



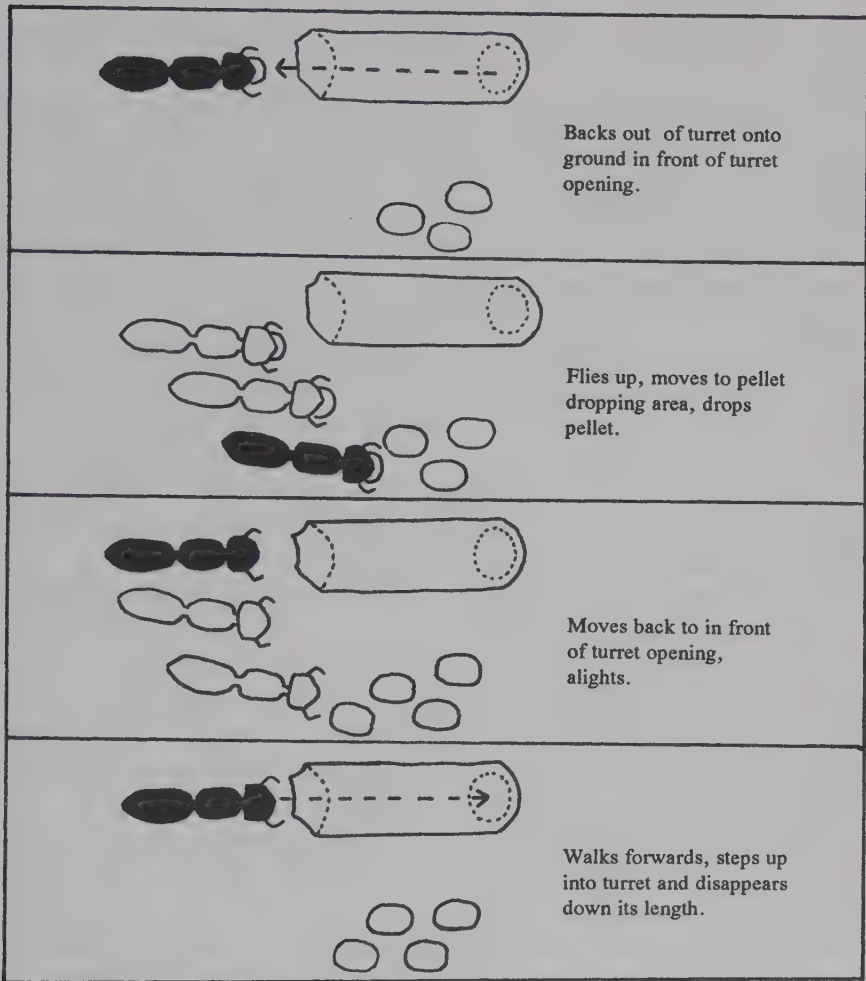


Figure 35. Method of pellet deposition after turret construction by *Ceramius capicola*.

served for *C. lichtensteini* but in different localities. The nesting aggregations of one population were littered with discarded pellets, whereas that of another was completely free from scattered pellets and the females were observed to fly to the edge of the clearing in which they were nesting and there to drop discarded pellets into the bushes.

After the "bulb" has been excavated the wasp is able to turn around in the nest and may emerge from the nest head first. Cycles of water carriage

and pellet extraction are performed rapidly and without interruption during active nest excavation.

Cell excavation having been completed, the cells of the Group 8 species are ready for oviposition whereas in the other groups a mud cell is first constructed within each excavated cell. Mud for the construction of these cells must be quarried within the nest as these wasps do not fetch mud from elsewhere. It is thought probable that mud used by *C. lichtensteinii* is obtained by deepening the lower end of the main shaft. In the nests of species of groups 3 and 6, the diameter of the "bulb" is greater the larger the number of cells, suggesting that mud for cell construction is probably quarried from the walls of the "bulb." The mud cells are constructed in such a way that the outer surface is rough and separate applications of mud are discernible whereas the inner surface is carefully smoothed (Fig. 27).

Each cell is sealed with mud after the completion of oviposition and provisioning. The seals of constructed mud cells are positioned just within the mouth of the cell. The outer surface of the mud plug is generally rough and convex (Fig. 28a). Those of *C. cerceriformis* (Group 2A) and *C. clypeatus* (Group 2B) are markedly concave.

After a cell has been sealed, the shaft above the cell is filled with earth until the vertical section of the shaft is reached. As no earth is carried into the nest, earth for filling must be obtained within the nest. After filling is completed a mud seal is constructed. This seal is smoothed so perfectly that it is not visible on the surface of the main shaft.

Further cells terminate secondary shafts and are prepared in a fashion similar to the first. The number of cells prepared is probably dependent in part on the availability of water for nest construction and pollen and nectar for cell provisioning, suitability of weather, and the constraints imposed by the nest architecture. Clearly the Group 5 nest plan allows for a greater number of cells to be excavated than does the Group 3 plan.

*Ceramius lichtensteinii* differs from the other species for which nest construction is known in that it continuously deepens the main shaft. This is possible because in its nests, unlike those of other species, the main shaft does not terminate in a cell.

#### REUSE OF NESTS

No evidence has been found of reuse of nests by wasps of groups 2 and 8, though reuse of nests seems to be the rule for wasps of groups 3, 5, and 6.

Insufficient information is available for comment to be made for groups 1, 4, and 7.

On emergence wasps of groups 3, 5, and 6 either initiate a new nest or enlarge the maternal nest. When several females emerge in a season, only one remains in the nest. All the others leave to initiate new nests. A reused nest is surmounted by a newly constructed turret. A new cell is constructed or a vacated cell is cleaned out and reused. In the case of a cell being reused the old cocoon is left in position. It seems that only the cell from which the possessor of the nest emerged is reused; all other cells and secondary shafts leading to them are freshly excavated.

I have established that a nest may be reused over a period of several years.

### *Ceramiopsis* Zavattari

There appears to be only one published record of the nesting of the Neotropical genus *Ceramiopsis*, that of *C. paraguayensis* (almost certainly a synonym of *C. gestroi* (Richards 1962)) entering a burrow in the ground, surmounted by a turret (Bertonni 1921).

### *Trimeria* Saussure

Nesting has been recorded for two species of the Neotropical genus *Trimeria*, *T. howardi* (Zucchi et al. 1976) and *T. buyssoni* (Neff and Simpson 1985). Both excavate burrows in the ground.

## NESTING AREAS AND NEST SITUATION

*T. buyssoni* was recorded as nesting in deep, hard open soil on an incline. No information was given concerning the nesting area of *T. howardi*.

## PROVISION

The provision of *T. howardi* was described as a food mass made from pollen and nectar. The mass was relatively solid with an irregular annulation, which probably corresponds to successive foraging trips.

The nature of the provision has not been established. Neff and Simpson (1985), however, describe pollen collection from flowers of species of Verbenaceae and Boraginaceae.

## WATER COLLECTION

Water collection has not been recorded, but water is most probably used in excavation to soften the "hard" soil.

## DESCRIPTION OF THE NEST

The nest of *T. howardi* is a nearly vertical burrow excavated in soil and surmounted by a vertical turret. A variable number of lateral shafts are excavated. Each terminates in at least one cell. Zucchi et al. claimed that some laterals are terminated by two or even three cells. The cells, which were horizontal, elongate ovals with the inner walls smooth and polished, were not constructed within excavated cells.

## REUSE OF NESTS

Reuse of nests is recorded.

*Microtrimeria* Bequaert

There appear to be no records of nesting by the Neotropical genus *Microtrimeria*.

*Masaris* Fabricius

The only recorded observations of nesting by the Palaearctic genus *Masaris* seem to be two conflicting accounts for *M. vespiformis*. Morice (1900) recorded having seen a female entering a simple burrow in flat sand. Doubt has been expressed by Richards (1962) as to the accuracy of Morice's observation. Richards is more inclined to support the allegation by Ferton (1920) that certain mud cells attached to rocks were those of this wasp. Ferton, however, though his allegation was supported by circumstantial evidence, neither saw a wasp entering the cells nor reared wasps from the cells.

*Pseudomasaris* Ashmead

Nesting has been recorded for eight species of the Nearctic genus *Pseudomasaris*, *P. coquilletti* (Richards 1963b), *P. edwardsii* (Torchio 1970),

*P. maculifrons* (Parker 1967), *P. occidentalis* (Hungerford 1937), *P. phaceliae* (Parker 1967; Torchio 1970), *P. texanus* (Bequaert 1940), *P. vespoides* (Torchio 1970), and *P. zonalis* (Parker 1967). All construct aerial earthen cells.

Dorr and Neff (1982) described a nest in a beetle boring. The nest consisted of a linear series of four unlined cells separated by mud partitions. This they alleged to have been a nest of *Pseudomasaris marginalis*, but they did not confirm the identity of the builder.

#### NESTING AREAS AND NEST SITUATION

Little information has been given on the nesting areas of *Pseudomasaris*. The fullest description is that given for *P. maculifrons* and *P. phaceliae*. These species were found nesting along the banks of a river between the levee and the riverbed. The soil was sandy and water-worn stones were common on the surface. There were patches of flowering *Phacelia congesta* (Hydrophyllaceae). *P. zonalis* was similarly found nesting near a stream but *P. coquilletti* was nesting on a rocky knoll and *P. vespoides* in an orchard. All but *P. vespoides*, which had constructed a nest on a twig, were nesting on stones. Where given, the position of the nests on the stones varied, those of *P. maculifrons* and of *P. zonalis* having been on the underside and those of *P. phaceliae* on the sides.

Some *P. edwardsii* were taken by Torchio from a grassy hillside on which *Phacelia leucophylla* was in flower and were kept in confinement in a greenhouse where they nested. The natural nesting situation was not recorded. In the greenhouse nest sites were always in open but concealed niches.

#### PROVISION

The provision of *P. maculifrons* and *P. phaceliae* was described as composed of pollen and nectar pellets tightly packed and that of *P. edwardsii* as a tacky, homogeneous mass of *Phacelia* pollen bound with *Phacelia* nectar and shaped into a solid cylinder (Torchio 1970, Figs. 4 and 10). Papilla-like projections were molded by *P. edwardsii* during the deposition of each load of pollen and nectar.

Flower associations (Chapter 3) indicate that the pollen and nectar of most species are derived either from *Penstemon* (Scrophulariaceae) or

*Phacelia* and *Eriodyction* (both Hydrophyllaceae), but that of some species may be of mixed provenance.

#### DESCRIPTION OF THE NEST

The nests of the *Pseudomasaris* species studied are composed of one or more elongate, parallel-sided earthen cells joined longitudinally to the substrate and to each other (Fig. 36 *top*). After cells are constructed additional soil is often placed over them as a complete covering (Torchio 1970, Figs. 2, 7, 17, 24).

The cell of *P. edwardsii* has been described in the greatest detail. It is a parallel-sided structure 14–21 mm in length and 5–6 mm in width. The walls vary in thickness from 0.25 mm to 1.0 mm, though wall thickness in any particular cell is constant. The outer surface bears a marked “fish-scale pattern” (Fig. 36 *bottom*) and the inner surface is smooth, unlined, and nonreflective. The cell cap is a plug of soil with a flat, unlined inner surface, usually of two concentric rings. Its outer surface is normally flat, smooth, and flush with the anterior margin of the cell. The thickness of the cell cap varies between 0.75 mm and 1.80 mm.

The cells attached to the substrate are incomplete and asymmetrical in cross section because the area of attachment is not coated with soil.

#### METHOD OF CONSTRUCTION OF THE NEST

The only account of cell construction, oviposition, and provisioning is that of Torchio for *P. edwardsii*.

Cell construction was initiated after the wasp had selected nest and soil-collection sites. At the soil-collection site soil was scraped up with the mandibles and collected together beneath the head. Nectar exuded through the folded mouthparts was rapidly absorbed into the soil until it was moist and adhered to the postgenal surfaces of the head. After the wasp had gathered a load of soil she flew back to the nest site. During cell construction, the returning wasp landed on the brim of the cell and curved her body until the posterior two or three abdominal sterna touched the outer surface of the brim. At the same time she thrust her head into the cell cavity until her mandibles, which appressed against the inner surface of the cell, were opposite the posterior abdominal sterna. As soil was deposited she moved her mandibles to shape the deposit while she simul-



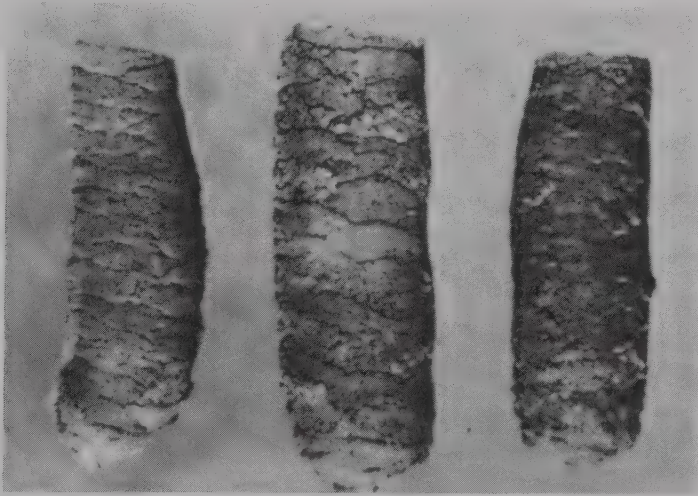


Figure 36. Nest of *Pseudomasaris edwardsii*: cluster of cells joined longitudinally (*top*); outer surface of cells showing "fish-scale pattern" (*bottom*) (from Torchio 1970).

taneously tamped the outer surface of the fresh deposit with her posterior abdominal sterna. Each deposit added to the cell during construction left an outline scar, which roughened the inner and outer surfaces of the cell wall. As construction neared completion, the wasp deposited the last few loads of soil within the cell and used them to smooth the inner surface.

After the completion of the cell, oviposition followed by provisioning takes place and the cell is then sealed.

Nest covering is very variable in extent.

### *Jugurtia* Saussure

Nesting has been recorded for two southern African species of the Afrotropical and Palaearctic genus *Jugurtia*, *J. confusa* (Gess and Gess 1980) and *J. braunsi* (Gess and Gess, unpublished fieldnotes). Both excavate a vertical burrow in the ground.

#### NESTING AREAS AND NEST SITUATION

*Jugurtia confusa* and *J. braunsi* nest in horizontal to sloping ground in areas of karroid scrub in relatively close proximity to their forage plants and a water source. One nest of *J. confusa* has been recorded as excavated in a pocket of soil on a ledge of a raised bank. This apparently unusual situation, however, falls within the category of horizontally presented soil.

The soil contains a sufficient clay factor that it is malleable when mixed with water. *J. confusa* nests are aggregated in bare areas. Those of *J. braunsi*, so far recorded, occurred singly in bare areas. It is probable that nesting was not in full swing, however, and that this species will also be found to nest in aggregations.

#### PROVISION

The provision of *J. confusa*, the only species of *Jugurtia* for which provision has been obtained, is a moist, sticky loaf composed of pollen and nectar. I examined microscopically pollen from the provision and compared it with pollen from flowers found in the vicinity of the nesting area. It was all of one type and matched that of *Drosanthemum floribundum* (Aizocaceae: Mesembryanthema). Available flower-visiting records indicate that the provision of *J. braunsiella*, *J. polita*, and *J. turneri* is most probably derived from

flowers of Asteraceae. That of *J. braunsi* is of uncertain provenance but most probably mixed, as this wasp has been found visiting flowers of Aizoaceae (*Mesembryanthema*), Asteraceae, and Campanulaceae.

#### WATER COLLECTION

Water for nest excavation is collected by *J. braunsi*, *J. braunsiella*, *J. confusa*, and *J. polita* females from saturated soil near the edge of a water source. Brauns (1905) observed *J. saussurei* similarly engaged.

#### DESCRIPTION OF THE NEST

The nests of *J. confusa* and *J. braunsi* consist of a subterranean burrow surmounted by a short, cylindrical mud turret (Fig. 37). The subterranean burrow consists of a vertical shaft of constant diameter for its entire length, from the lower end of which there branches a short subhorizontal shaft terminating in an excavated cell, within which is a constructed mud cell.

Of the nests which I excavated only one, a nest of *J. confusa*, was at a more advanced stage of construction. In this nest further subhorizontal secondary shafts, each terminating in a cell, were present (Fig. 37b). Each secondary shaft including a cell was barely longer than the cell itself. All completed cells were sealed with a mud plug constructed within the neck of the cell like a cork in a bottle.

#### METHOD OF CONSTRUCTION OF THE NEST

Nest excavation is initiated when the female regurgitates water from her crop onto the ground. Using her mandibles she works this water into the earth to form mud, from which she forms a pellet. A number of pellets is formed in this way from each cropfull of water. The first pellets excavated from the shaft-initial may be discarded (Fig. 38). The shaft-initial is circular in cross section because the female rotates evenly, not altering the direction of rotation without first completing a circle. At the commencement of turret construction, the pellets, instead of being discarded, are laid down in a circle around the shaft-initial in such a way that the inner

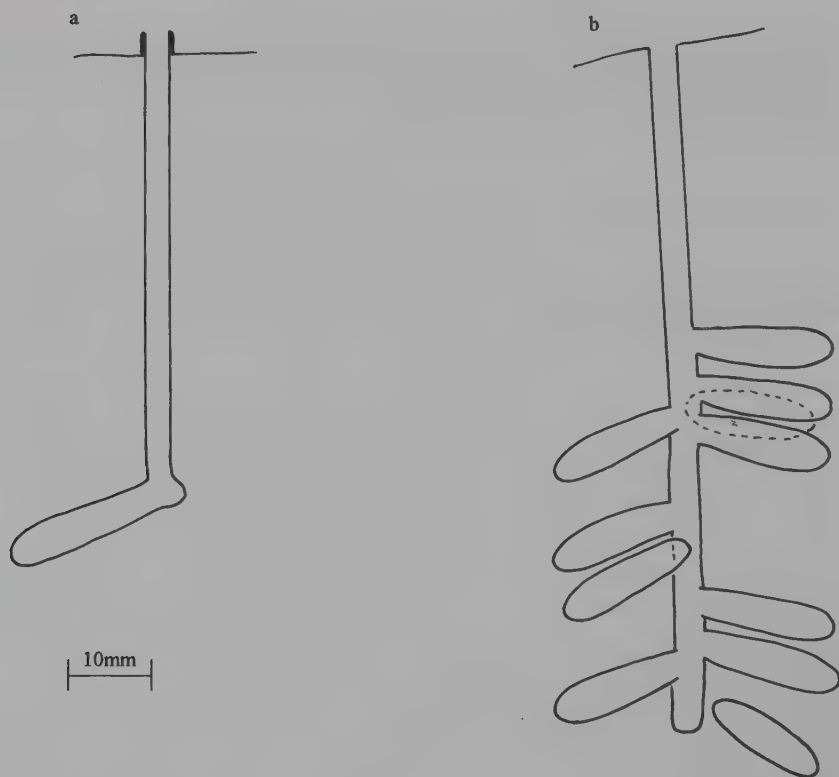


Figure 37. Vertical plans of turrets and underground workings of nests of *Jugurtia confusa*, Hilton, Grahamstown: (a) newly constructed nest; (b) reused nest, with no cell terminating the main shaft.

diameter of the turret will be the same as that of the shaft. Additional pellets are added regularly so that the resultant turret is a vertical cylinder.

After completion of the turret the wasp continues to excavate the shaft but the pellets then extracted are discarded. *J. confusa* has no clearly defined pellet-dropping area, but the wasp does confine her arrivals at and departures from the nest to a set quarter segment.

Cycles of water carriage and pellet extraction are performed rapidly and without interruption during active nest excavation.

Shaft diameter is maintained constant so that there is no "turning bulb" such as is formed by *Ceramius*. In consequence the wasp continues to emerge backward throughout shaft excavation.



From the bottom of the main shaft a secondary shaft is excavated in a subhorizontal plane in such a way that the distal end lies deeper than the bottom of the main shaft and is enlarged to form a cell. A mud cell is constructed within the excavated cell. Mud for the construction of such a cell must be quarried within the nest, as mud is not brought into the nest. In nests of *J. confusa* in which a mud cell has been constructed there is an enlarged "heel" at the bottom of the shaft. It is thought probable that at least part of the soil used in constructing the mud cell is excavated from this source. The mud cells are constructed in such a way that the outer surface is rough and separate applications of mud are discernible whereas the inner surface is carefully smoothed. The average thickness of the walls is 0.7 mm.

After oviposition and provisioning the cell is sealed with mud. The remaining section of the secondary shaft is filled with earth and sealed off from the main shaft with mud, which is smoothed so that the entrance to the secondary shaft is no longer visible.



Figure 38. *Jugurtia confusa* extracting mud from shaft-initial, turret in early stage of construction.

Succeeding cells are constructed in the same manner, the number probably being dependent on the availability of water for nest construction and pollen and nectar for cell provisioning.

#### REUSE OF NESTS

I found evidence for reuse of nests by *J. confusa*. A nest marked at the end of one summer season was at the start of the following season being worked upon by a freshly emerged female, which had furnished it with a new turret. Sunning himself in the vicinity of the nest was a freshly emerged male. On excavation I found that eight of the eleven cells were open, empty, and lined with parchment. They were therefore clearly cells from a previous year's nesting season.

#### *Masarina* Richards

Nesting has been recorded for one species of the Afrotropical genus *Masarina*, *Masarina familiaris* (Gess and Gess 1988a). This wasp excavates a multicellular subhorizontal burrow in vertical earth banks. Since we investigated the nesting of *M. familiaris*, however, Fred and I have made some observations on the nesting of a single individual of *M. strucki* which indicate that the nesting of *M. familiaris* may not be typical for all species of the genus.

#### NESTING AREAS AND NEST SITUATION

*Masarina familiaris* has been recorded nesting at three sites to the west of the Olifants River Valley, all in dry fynbos and in an area of mixed dry fynbos and karroid scrub and in relatively close proximity to a water source. It has been recorded nesting in banks (Gess and Gess 1988a, Figs. 1–3) varying in height from 15 to 100 cm. The nests were sited at heights of a few centimeters to half a meter. The soil of the nesting sites varied from a sand-colored clay-sand mixture with a relatively low proportion of clay to a hard, nonfriable, red clay-sand mixture with a relatively high proportion of clay. In all cases the soil was malleable when mixed with water.

The nests occurred singly and also grouped in the vicinity of an old nest, suggesting that there is a tendency for a newly emerged female to initiate a nest in close proximity to the nest from which she herself emerged.



## PROVISION

The provision, a mixture of pollen and nectar, is very wet and sticky. Being wet, it has no discrete shape of its own. It occupies about two-thirds of the cell.

In the Clanwilliam district (Fig. 8) pollen for provisioning was derived solely from flowers of one or more *Aspalathus* species (Papilionaceae), the only flowers on which *M. familiaris* has been observed foraging in that district. It is possible, however, that in other areas pollen from *Lebeckia* and *Wiborgia* (both also Papilionaceae) may be used, as *M. familiaris* has been recorded foraging on these plants in the Springbok area (Fig. 8).

Foraging records indicate that it is probable that the provision of *M. mixta* and an undescribed species is derived from *Wahlenbergia* (Campanulaceae).

## WATER COLLECTION

Water for nest construction is collected by females from saturated soil at the edge of a water source.

## DESCRIPTION OF THE NEST

The nest of *M. familiaris* consists of a multicellular burrow with a downwardly curved tubular mud turret at its entrance (Fig. 39). The turret (Gess and Gess 1988a, Fig. 4) is constructed of mud pellets smoothed on the inside but left rough on the outside. A large number of interstices are left open so that the turret has a somewhat lacy appearance. The turret and shaft entrance are of the same diameter. There are one or more subhorizontal to upwardly or downwardly sloping shafts, each ending in a cell. All shafts leading to sealed cells are filled with earth and sealed with a mud plate a short distance inside the burrow entrance. A cell is, over most of its length, of the same diameter as the shaft. There is a distinct neck of smaller diameter than that of the cell and shaft. Distally the cell walls slope inward abruptly to a truncate end wall.

## METHOD OF CONSTRUCTION OF THE NEST

Water is required for nest construction. At an early stage in burrow excavation turret construction is initiated using pellets extracted from the

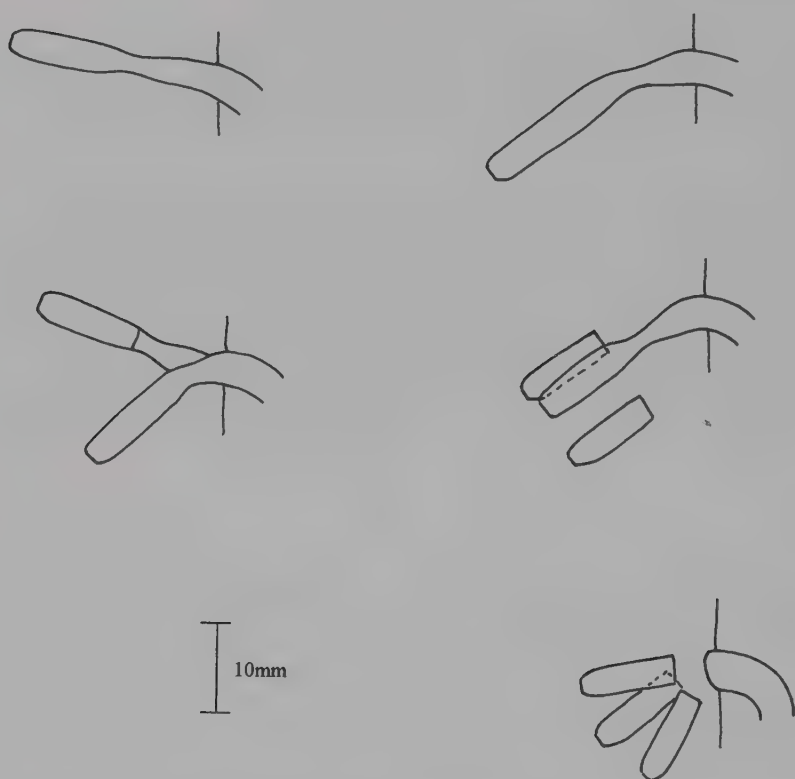


Figure 39. Vertical plans of turrets and underground workings of *Masarina familiaris*.

excavation. At the commencement of turret construction pellets are laid down around the shaft opening in such a way that the turret will have the same diameter as the shaft. Almost from the start additional pellets are added in such a way that the turret curves over and downward. After turret construction has been completed, further pellets extracted from the excavation are dropped so that they accumulate in a pile at the base of the bank beneath the nest.

The shafts are short and generally slope downward, although they less commonly slope upward (in a sample of 15, 13 sloped downward and two upward). The average angle of slope for the sample was  $26^\circ$ . A shaft is extended without change of angle to end in a cell. Cell excavation is preceded by a reduction of 1 mm in the diameter of the shaft over a short distance to form a neck. After the neck has been created the diameter returns to that of

the shaft until the inner end of the cell is approached, so that the cell walls are parallel over most of the length of the cell. Shortly before the end of the cell is reached, there is a rapid reduction in diameter so that the sides slope inward to the end of the cell, which is truncate, not curved.

The excavated cell is very carefully smoothed and shaped so that, although a mud cell is not constructed within it, the walls of the cell are stabilized to such a degree that in nests constructed in relatively friable soils parts at least of the cell walls can be separated from the surrounding soil.

After oviposition and provisioning the cell is sealed with a thin mud plate and the shaft is filled with earth. Several secondary shafts, each terminating in a cell, may be similarly excavated and completed.

#### REUSE OF NESTS

No indication has been found of reuse of nests.

#### *Celonites* Latreille

Nest construction has been recorded for seven, possibly eight, species of *Celonites*.

Aerial earthen cells on stones or plant stems are constructed by five of these: three Palaearctic species, *C. abbreviatus* (Lichtenstein 1869, as *C. apiformis* Fabricius; Ferton 1901, 1910; Fahringer 1922; Bellmann 1984), *C. fischeri* (Bingham 1898), and *C. mayeti* (Lichtenstein 1875; Ed. André 1884); a Palaearctic/northern Afrotropical species, *C. jousseaumei* (Richards 1962); and an Afrotropical species, *C. andrei* (Brauns 1913). In addition mention is made in Gess and Gess (1989) of an aerial nest, a putative nest of *C. promontorii*.

Earthen cells are constructed in a pre-existing burrow by one species, *C. wahlenbergiae* (Gess and Gess 1992), and a burrow, in which is constructed an earthen cell, is excavated by another, *C. latitarsis* (Gess and Gess 1992).

#### NESTING AREAS AND NEST SITUATION

Little information seems to be available concerning the nesting areas of the aerial-nesting *Celonites* species. Bellmann (1984) noted that *C. abbrevi-*

*viatus* was nesting in rocky or stony dry meadows. *C. andrei* and *C. promontorii* are wasps of karroid scrub. Nesting situation may be variable, nests of *C. abbreviatus* being situated under and on the sides of stones and on rocks at heights of 1–2 m (Bellmann 1984), on dry plant stems (Lichtenstein 1869), and under bark (Fahringer 1922).

The areas in which the two ground-nesting species were investigated is open dry fynbos. The soil is sandy, relatively coarse, and loose on the surface but finer and more compact beneath. The finer sand is brought to the surface by the Cape Dune Molerat, *Bathyergus suillus* (Schreber) (Bathyergidae). The molehills stabilize to form "hillocks" of compacted sand in which the wasps nest.

#### PROVISION

The provision of *C. abbreviatus* examined by Bellmann (1984) was orange and of a honey-like ("honigartiger") consistency. This "honey" was in contact with the cell walls only at isolated points, and its surface was divided by furrows into portions representing provision loads, which would indicate that it was of a firm consistency. The pollen was not identified, but Bellmann stated that *Teucrium montanum* (Lamiaceae) was favored for the collection of pollen and nectar in the area where nesting was studied. Schremmer (1959) observed the collection of pollen and nectar from *Salvia officinalis* (also Lamiaceae) in Istria, Yugoslavia.

The provision of *C. wahlenbergiae* which I examined was olive green, and though it was very moist it did not adhere to nor wet the cell walls. The pollen, which I examined microscopically, was of two types, both apparently smooth-walled. On comparison with pollen from plants growing in the vicinity of the nest, one of the pollens was found to match only that from *Wahlenbergia paniculata* (Campanulaceae) and the other only that from a *Coelanthus* (Aizoaceae) species which was growing mixed with the *Wahlenbergia*. Although *Crassula dichotoma* (Crassulaceae) was visited by the nester, there was no pollen from this plant in the sample of provision examined. It is possible that it was being visited for nectar only.

As provision has been obtained only from Clanwilliam (Fig. 8), no comment can be made on whether any of the other plants visited by the

wasp in other areas was being made use of for obtaining pollen and/or nectar for provision.

Pollen from the provision of *C. latitarsis* was all of one type. On comparison with pollen from plants growing in the vicinity of the nest, I found that it matched only that of *Wahlenbergia psammophila* (Campanulaceae).

#### DESCRIPTION OF NEST

The aerial nests consist of a group of earthen cells in close proximity to each other. The arrangement of the cells is variable even within species. The cells of *C. abbreviatus* described by Bellmann (1984) are abutted lengthwise, for example, and those described by Lichtenstein (1869) end to end, sometimes with another row parallel to the first. Completed groups of cells are either left uncovered (Richards 1962, based on the accounts available to him) or are covered with a common layer of earth (Fig. 40a) about as thick as the cell walls, the spaces between the cells being left as cavities (Bellmann 1984). The cells seem to be most commonly oriented vertically, opening downward and less commonly inclined to horizontal.

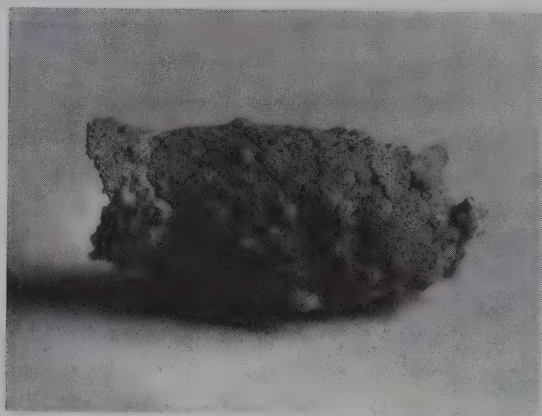
Of the ground nesters, the nest of *C. wahlenbergiae* consisted of three linearly arranged earthen cells attached to the wall of an apparently pre-existing burrow excavated in sandy soil (Fig. 41). The three cells, two completed and sealed and the third in an early stage of construction (Figs. 40b and c), were of a diameter appreciably less than that of the burrow. The nest of *C. latitarsis* consisted of an arched entrance leading to a short sloping burrow terminating in a horizontal excavated cell (Fig. 42). Within the excavated cell and of the same diameter was a constructed earthen cell (Fig. 40d).

Apparently characteristic of all species is the distinct "fish scale" pattern on the outer surface of the constructed earthen cell. All cells are rounded at the closed end and somewhat truncate at the open end. A seal is positioned just inside the cell opening. The cells from the nests of *C. wahlenbergiae*, *C. latitarsis*, and the putative nest of *C. promontorii* are ovoid, whereas those of *C. abbreviatus* figured by Bellmann are almost parallel-sided. The constructed walls of most of the cells investigated by Bellmann were incomplete, the substrate forming part of the cell wall.





*Figure 40a.* Putative nest of *Celonites promontorii* ( $\times 3$ ).



*Figure 40b.* Cell of *Celonites wahlenbergiae* ( $\times 5$ ).

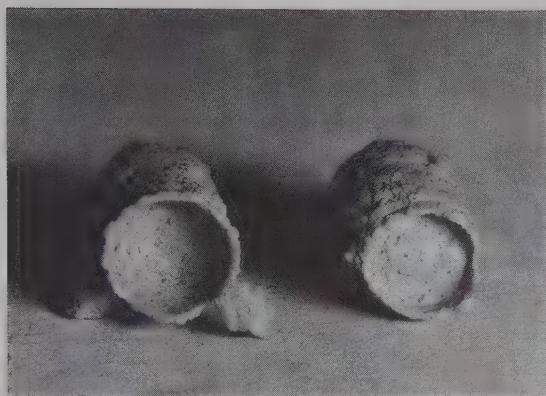


Figure 40c. *Celonites wahlenbergiae*: incomplete cell with rounded blind end (left) and sealed completed cell (right) ( $\times 4.2$ ).



Figure 40d. Cell of *Celonites latitarsis* ( $\times 4.5$ ).

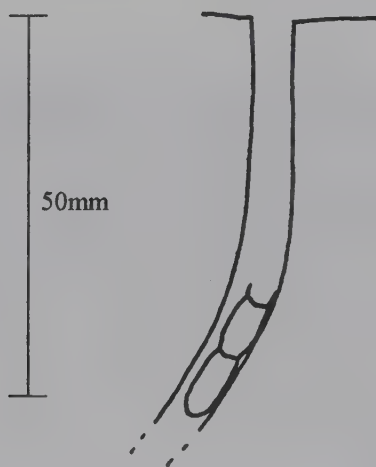


Figure 41. Vertical plan of nest of *Celonites wahlenbergiae*.

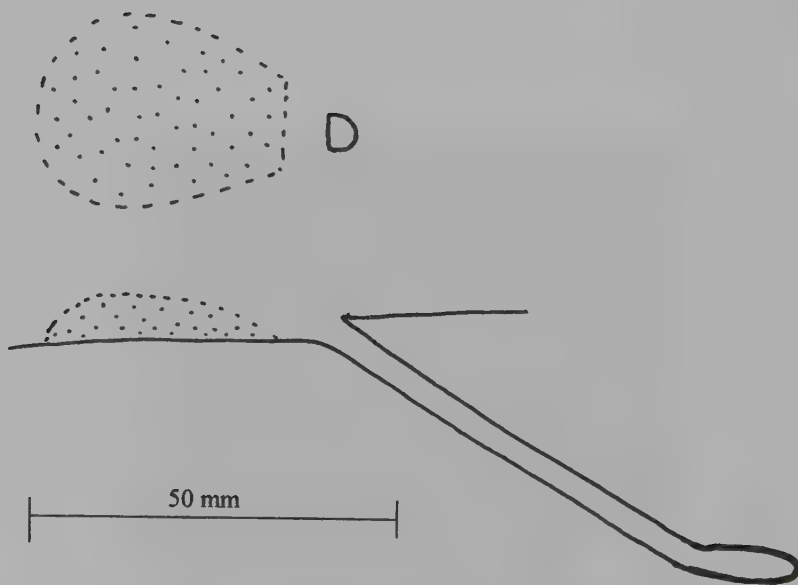


Figure 42. Nest of *Celonites latitarsis*: nest entrance and tumulus as seen from above (top); vertical plan (bottom).

## METHOD OF CONSTRUCTION OF THE NEST

From a consideration of the observations of Bellmann (1984) and Gess and Gess (1992), it seems likely that the method of cell construction is similar in all species. While building a cell a wasp makes regular visits to a quarry site. The quarry sites of the two ground-nesting species observed by us were on stabilized molerat hillocks, 2.5 m (*latitarsis*) and 3 m (*wahlenbergiae*) from the nests. At the quarry site the wasp vibrated up and down vigorously while scraping up a load of sand, which was held by the mouthparts. The visits to the quarry alternated regularly with periods in or at the nest during which building material was added to the cell. Alternating with a cycle of visits to the quarry and the nest (five to seven observed for *latitarsis*) were periods away to collect liquid to mix with the dry sand to make it malleable for cell construction. As the cell walls are harder and more durable than they would be had water been used, and as *Celonites* has never been observed at water, it seems probable that nectar is used. Certainly between bouts of quarrying and cell construction *C. latitarsis* regularly visited a succession of *Wahlenbergia psammophila* flowers.

Each load of earth is added to the cell in the form of a semi-circular plate. Bellmann observed that when a *C. abbreviatus* female is building she positions herself with her head inside the cell and her abdomen curved around on the outside. I monitored cell construction by *C. latitarsis* from start to finish. It took approximately two hours, during which time 36 additions to the cell were made. Each visit to the quarry took 29 seconds ( $n = 36$ ) and each period in the nest during which cell construction proceeded took 48 seconds ( $n = 37$ ). Absences for liquid collection took 10–20 minutes.

After oviposition and provisioning have been completed the cell is sealed with a plate constructed just inside the lip of the cell from moistened earth laid down in concentric rings.

Further cells may then be constructed. After the completion of the construction of a group of aerial cells, the builder may bring further "mortar" for the construction of a covering.

In nest construction by *C. latitarsis*, cell construction is preceded by burrow excavation. Sand excavated from the burrow is drawn out by the wasp as she reverses out of the burrow. Excavated sand accumulates as a tumulus approximately 20 mm downslope from the burrow entrance.

From time to time a certain amount of raking of the "path" between the burrow and the tumulus takes place. The burrow entrance is left open while the wasp is away from the nest.

### *Quartinia* Ed. André

Previous to the account of the nesting of *Q. vagepunctata* (Gess and Gess 1992), the only record of nesting by *Quartinia* was the observation of Jacot Guillarmod (pers. comm.) that he had seen the burrows of a *Quartinia* species in garden soil. The presence or absence of turrets was not mentioned. There appear to be no records of nesting by the Palaearctic species of *Quartinia*.

### NESTING AREA AND NEST SITUATION

The nesting site of *Q. vagepunctata* was a bare patch, approximately 1 m square, of somewhat uneven level ground between shrubs in an area of karroid scrub. The soil was sandy and friable. Each nest had its entrance to one side of an earth clod or stone (Fig. 43).

### PROVISION

The provision from each of four nests of *Quartinia vagepunctata* was in the form of a relatively moist, bright yellow nectar and pollen mass almost entirely filling the cell, adhering to the cell walls and therefore not forming a discrete pollen loaf. The pollen from one of the nests was found to be all of one kind and to match that of *Cotula cf. leptalea* (Asteraceae). That from the other three nests matched that of *Relbania* and *Cotula* (both Asteraceae).

### DESCRIPTION OF THE NEST

The nest consists of a subterranean silk-lined burrow surmounted by a horizontal turret constructed from silk and sand (Fig. 44), the inner surface being of silk and the outer surface of sand (grain size: 0.16–1.2 mm) held together by the silk.

The turret is bag-like, approximately circular in cross section with its diameter greatest at its outer open end and smallest at its closed inner end.





Figure 43. *Quartinia vagepunctata* nesting site; arrow indicates sand and silk nest entrance turret.

The opening to the burrow entrance is at some little distance from the closed inner end of the bag (Fig. 45).

The burrow consists of a subvertical shaft, which terminates in a sealed, roughly ovoid cell. The cell walls are constructed of sand bonded together with silk and well cemented with a substance somewhat resinous in appearance. In one of the nests the female was found sheltering in a lateral shaft, which would suggest that more than one cell per nest is probably constructed.

#### METHOD OF CONSTRUCTION OF THE NEST

The soil in which the nest is excavated is friable. Water is not required for nest excavation and is not used as a bonding agent. It is therefore not surprising that *Q. vagepunctata*, though collected commonly at flowers, has never been collected at water.



Figure 44. *Quartinia vagepunctata*, dorsal view of nest entrance turret.

The silk used in nest construction is spun by the nest builder. One individual was observed while it was joining together sand grains with silk. It was rotating its head and the silk was apparently issuing from its mouth.

The nature of and provenance of the substance used in conjunction with silk in the bonding of the cell walls has not been determined.

#### *Quartinioides* Richards

The only observation concerning the nesting of the Afrotropical genus *Quartinioides* seems to be that of Gess and Gess (1988a, 1989). We found vertical burrows in friable coastal dune sand. The burrows were not surmounted by turrets.

#### *Quartiniella* Schulthess

There appear to be no records of nesting by this Afrotropical genus.

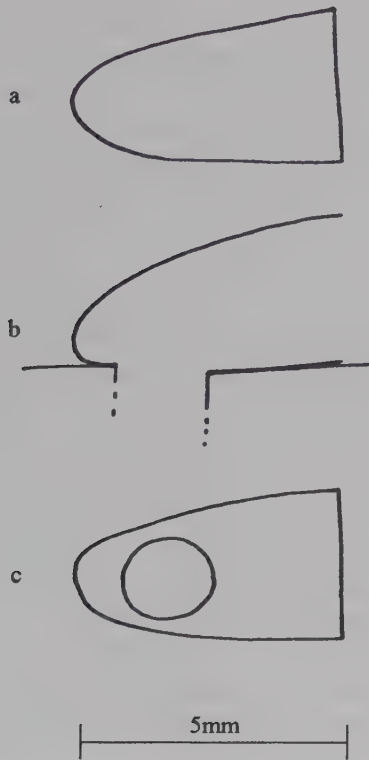


Figure 45. *Quartinia vagepunctata*, plans of turret: (a) from above; (b) vertical section; and (c) from below.

### *Overview of nesting by the masarines as a group*

#### Nest situation and basic nest type

In considering the structuring of aculeate wasp and bee communities, Fred (Gess 1981) devised a classification for aculeate wasps and bees based on ethological characters. In this classification four basic nesting situations were recognized: the ground, vertical banks, stones, and plants. Nesters in soils were divided into two main types, nesters in friable soil and nesters in nonfriable soil, and nesters associated with vertical banks and plants were divided into those nesting in or on the substrate. All four basic nesting situations and both the basic soil types have been exploited by masarine wasps.

The basic form of self-excavated nest prepared by aculeate wasps is a single-celled burrow dug in friable soil. This basic nest type, typical of some sphecids and pompilids, has not been recorded for any masarines. Derived from this nest type are multicellular nests of varied architecture dug in friable soil. From this nest type is derived nest excavation in nonfriable soil with the adoption of the use of water for softening the soil and usually with the use of some of the spoils of excavation for the construction of a turret surmounting the burrow entrance. The prevalence of nesting in nonfriable soil by masarines is matched only by the Eumeninae, although it is not uncommon among the bees. In the Sphecoidea and Pompilidae, although ground nesting is common, indeed the greatest number of ground-nesting species is to be found among the sphecoids, only one genus each is known to have species nesting in nonfriable soil and surmounting the burrow with a turret, *Bembecinus* (Nyssonidae) (Gess and Gess 1975) and *Dichragenia* (Pompilidae) (Gess and Gess 1974, 1976b). Even in the large genus *Bembecinus*, nesting in nonfriable soil is the exception, having been recorded for only two species. Clearly the habit of nesting in nonfriable soil, using water in excavation, and surmounting the burrow with a turret must have evolved independently in the Apoidea, Sphecoidea, and Pompilidae. It seems probable, however, that it is ancestral for both the Eumeninae and the Masarinae in the Vespidae. This probability may possibly be supported by the fact that the only nesting recorded for the Euparagiinae is for a ground nester which surmounts its burrow with a turret (Williams 1927; Clement and Grissell 1968), though the methods employed in burrow excavation and turret construction are not clear. Certainly nesting in friable soil by *Pterocheilus* (Eumeninae) and *Rolandia* and *Celonites latitarsis* (Masarinae) is derived.

In all groups, nesting in vertical banks—which is seen as distinct from nesting in horizontal ground, as no species are known to nest in both situations—is less common than nesting in the ground. It, however, seems to be exceptionally uncommon in the Masarinae, being known only for *Masarina*.

Both excavating burrows in living tissue, as exemplified by *Dasyproctus* species (Crabronidae), and excavation of burrows in dead plant tissue, as exemplified by the Xylocopinae (Anthophoridae), are unknown in the Masarinae.

Nesters on plants together with nesters on stones are associated with the substrate merely as a suitable support for the nest, the nesting materi-



als not being derived from the substrate but brought to it. As noted, such nesters have arisen several times among the higher masarines. They are also to be found among the eumenines and the social wasps in the Vespidae, the Pompilidae, and the Sphecoidea.

In Fred's classification nesters in all situations are divided into three categories based on the degree of participation in the construction of the nest: nest constructed entirely by the nester; pre-existing cavity modified by the nester; and pre-existing cavity not modified by the nester.

The pollen wasps for which nesting is known almost all fall into the category "nest constructed entirely by the nester." The only masarine known to modify a pre-existing cavity is *Celonites wahlenbergiae*, nesting as it does in a pre-existing cavity in the ground (Gess and Gess 1992). Nesting in a pre-existing cavity in logs by *Pseudomasaris marginalis* has been claimed by Dorr and Neff (1982), but unfortunately the identity of the nester was not confirmed. When discussing the *Quartinia* group Richards (1962) stated that he would "not be surprised if they nested in hollow stems." As yet, however, no evidence of nesting in such situations has been found, the only three species for which nesting situation is known being ground nesters (Gess and Gess 1992). Nesting in pre-existing cavities modified by the nester is not uncommon in the vespid subfamily the Eumeninae and, furthermore, occurs in the pompilids and is common among the sphecoids and the bees.

Nesters in "pre-existing cavities not modified by the nester" include those species which provision a cavity without preparing the cavity in any way, principally Scoliidæ and Tiphiidæ, and those species which are labor parasites ovipositing into a nest provisioned by an individual of another species. The latter category of nesting is typical of the Chrysididæ and is found among the sphecoids and the bees. The unusual form of the abdomen which gives *Celonites* the ability to roll itself in the manner of the Chrysididæ led to the assumption that it would be found to be a nest parasite of other Hymenoptera in the chrysidid manner (Saussure 1854). However, this was, as has been shown (Chapter 4), an erroneous assumption.

## Classification of masarine nest types

From an analysis of the nesting accounts it is possible to recognize seven basic nest types and to allocate 42 species to these nest types as listed below.



*Nest Type 1* A multicellular subvertical burrow in horizontal to subhorizontal ground excavated by the nester, with or without an entrance turret, and with the excavated cells not containing constructed cells:

*Type 1A* Excavated with the use of water:

four species of *Ceramius*: all species of Group 8 (*C. capicola*, *C. linearis*, *C. bicolor*, and *C. socius*); and one species of *Trimeria*: *T. howardi*.

*Type 1B* Excavated without the use of water:

two species of *Rolandia*: *R. angulata* and *R. maculata*.

*Nest Type 2* A multicellular subhorizontal burrow in vertical to subvertical ground excavated by the nester, with an entrance turret constructed from earth extracted from within the burrow, and with the walls of each excavated cell lined with cemented earth excavated within the burrow:

one species of *Masarina*: *M. familiaris*.

*Nest Type 3* A multicellular subvertical burrow in horizontal to subhorizontal ground excavated by the nester, with or without an entrance turret constructed from earth extracted from within the burrow, and with each excavated cell containing a constructed cell formed from earth excavated within the burrow:

three species of *Paragia*: *P. (Paragia) tricolor*, *P. (Paragia) decipiens*, and *P. (Cygnea) vespiformis*;

eleven species of *Ceramius*: Group 2A (*C. cerцерiformis*); Group 2B (*C. clypeatus*); Group uncertain, probably 2B (*C. micheneri*); all species of Group 3 (*C. nigripennis*, *C. jacoti*, *C. braunsi*, and *C. toriger*); the single species of Group 5 (*C. lichtensteinii*); Group 6 (*C. rex* and *C. metanotalis*); Group 7 (*C. tuberculifer*); and two species of *Jugurtia*: *J. confusa* and *J. braunsi*.

*Nest Type 4* A group of constructed cells attached to plant stems or stones: six species of *Celonites*: *C. abbreviatus*, *C. fischeri*, *C. mayeti*, *C. jousseaumei*, *C. andrei*, and probably *C. promontorii*; eight species of *Pseudomasaris*: *P. coquilletti*, *P. edwardsii*, *P. maculifrons*, *P. occidentalis*, *P. phaceliae*, *P. texanus*, *P. vespoides*, and *P. zonalis*; and one species of *Gayella*: *G. eumenoides*.

*Nest Type 5* Constructed cells located in a pre-existing cavity; soil for cell construction is collected from a quarry site at some distance from the nest:

one species of *Celonites*: *C. wahlenbergiae*.

*Nest Type 6* A self-excavated sloping burrow in friable soil with an excavated cell in which is an earthen cell constructed from soil collected from a quarry site at some distance from the nest:

one species of *Celonites*: *C. latitarsis*.

*Nest Type 7* A subvertical silk-lined burrow in friable soil, surmounted by a silk and sand turret and having an excavated cell in which is a constructed sand and silk cell:

one species of *Quartinia*: *Q. vagepunctata*.

Ground nesting has been recorded for an additional nine species: *Paragia* (*Paragia*) *smithii*; *Riekia* sp.; *Ceramiopsis paraguayensis*; three species of *Ceramius*—Group 1, *C. fonscolombei* and *C. biscoffi*, and Group 4, *C. beyeri*; one species of *Trimeria*, *T. buyssoni*; a species of *Quartinia* sp.; and *Quartinoides* sp. H. However, the observations are too incomplete for determination of nest type.

Nest characters can be used to test groupings based on morphological characters. For example, they can be applied to test the validity of the species groups within the genus *Ceramius*:

- |   |  |         |
|---|--|---------|
| 1 | Excavated cells not containing constructed cells . . . . .   | Group 8 |
| — | Excavated cells containing constructed cells . . . . .       | 2       |
| 2 | No cell terminating main shaft . . . . .                     | Group 5 |
| — | Cell terminating main shaft . . . . .                        | 3       |
| 3 | Cells subvertical . . . . .                                  | Group 3 |
| — | Cells subhorizontal . . . . .                                | 4       |
| 4 | "Bulb" short, bottom end well above level of cells . . . . . | Group 2 |
| — | "Bulb" long, bottom end level with cells . . . . .           | Group 6 |

Groups 1, 4, and 7 have been omitted as to date insufficient data have been recorded.

An interesting nest character is cell shape. The blind ends of the cells of *Masarina familiaris* are markedly truncate, whereas the blind ends of the cells of the *Paragia*, *Ceramius*, *Pseudomasaris*, *Jugurtia*, and *Celonites* species for which they are known are rounded. This difference, together with the situation of the nests in vertical banks and the attachment of the egg, sets the nests of *M. familiaris* apart from those known for the closely related genus *Jugurtia*.

### Bonding agent

Three bonding agents—water, nectar, and silk—are known to be used by masarines in nest construction.

Use of water in excavation and as the bonding agent is either stated or implied in all nesting accounts of Nest Types 1A, 2, and 3. In addition, the inner surfaces of the cells of *Trimeria howardi* are polished (Zucchi et al. 1976) and those of *Paragia* (*P.*) *tricolor* are polished and waterproofed (Houston 1974) with unidentified substances.

Nectar is the proven bonding agent employed by *Pseudomasaris edwardsii* of Nest Type 4 (Torchio 1970). Circumstantial evidence furthermore suggests that nectar is used by *Celonites* of Nest Types 4, 5, and 6 (Gess and Gess 1992).

The use of self-generated silk sets Nest Type 7, as exemplified by *Quartinia vagepunctata*, apart from all the others (Gess and Gess 1992). The use of silk in nest building by wasps seems to be altogether uncommon. It has been noted for two eumenines, one ground-nesting (Gess and Gess, unpublished fieldnotes) and one nesting in pre-existing cavities (Weaving, pers. comm.), and has been recorded for two social pemphredonids, one constructing aerial nests, *Microstigmus comes* Krombein (Myers 1934; Matthews and Starr 1984) and one nesting in pre-existing cavities, *Arpactophilus mimi* Naumann (Matthews and Naumann 1988). The adult pemphredonids secrete the silk from glands near the tip of the metasoma. Adult *Q. vagepunctata* observed appeared to produce silk from their mouths.

Using nectar or silk as a bonding agent frees the user from dependence on water, an often ephemeral resource in arid areas. The use of silk furthermore makes it possible for the users to construct nests in and with friable soil, which otherwise becomes readily unstable under dry conditions.

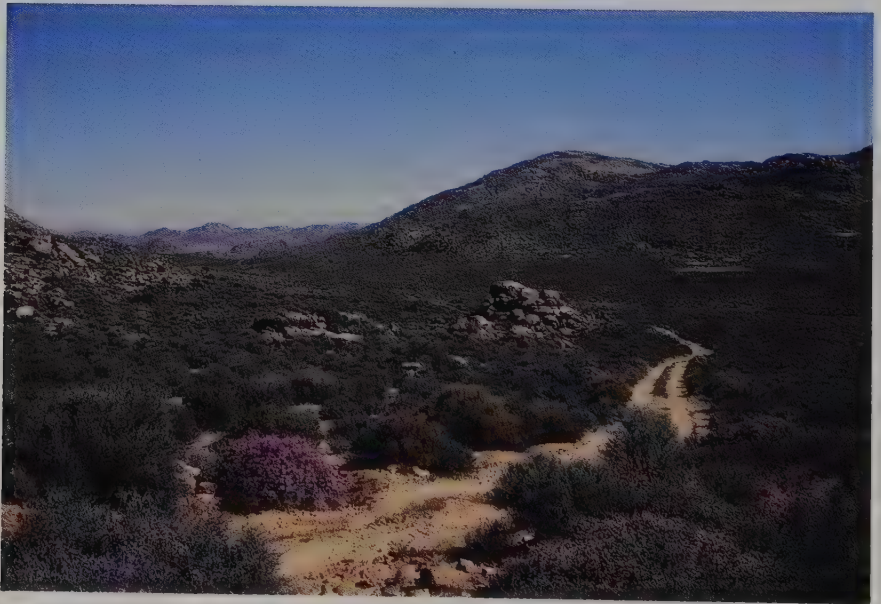


*Ceramius lichtensteinii* (Klug).





*Plate 1.* Lower reaches of the Nossob River Valley, Kalahari Gemsbok National Park, an area at the interface between the Karoo and Savannah Biomes.



*Plate 2.* Goegab Nature Reserve, Springbok, Namaqualand, in an area of Namaqualand Broken Veld (Acocks Veld Type 33).

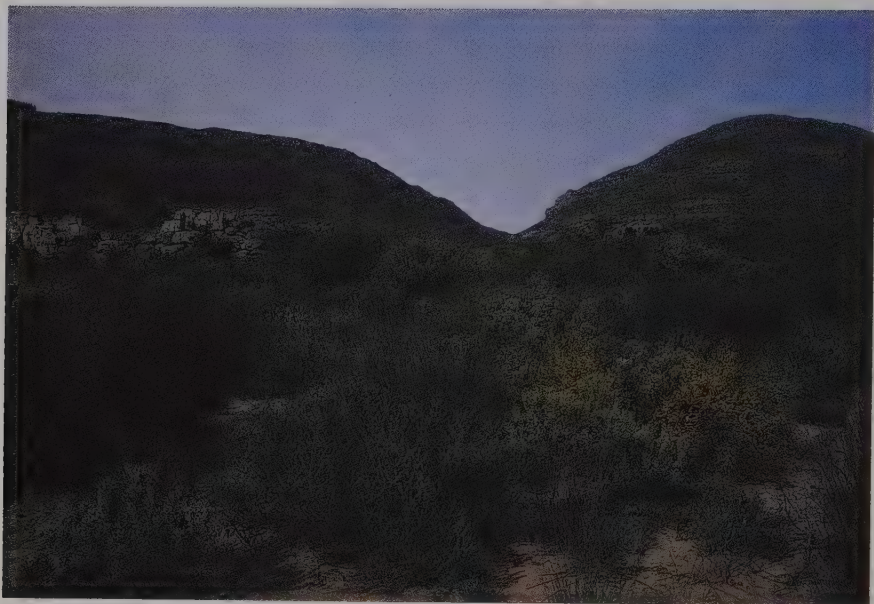




*Plate 3.* Skuinshoogte Pass, 15 km north of Nieuwoudtville, in an area of Western Mountain Karoo (Acocks Veld Type 28).



*Plate 4.* Caleta Cove, Clanwilliam, in an area of Karroid Broken Veld (Acocks Veld Type 26).

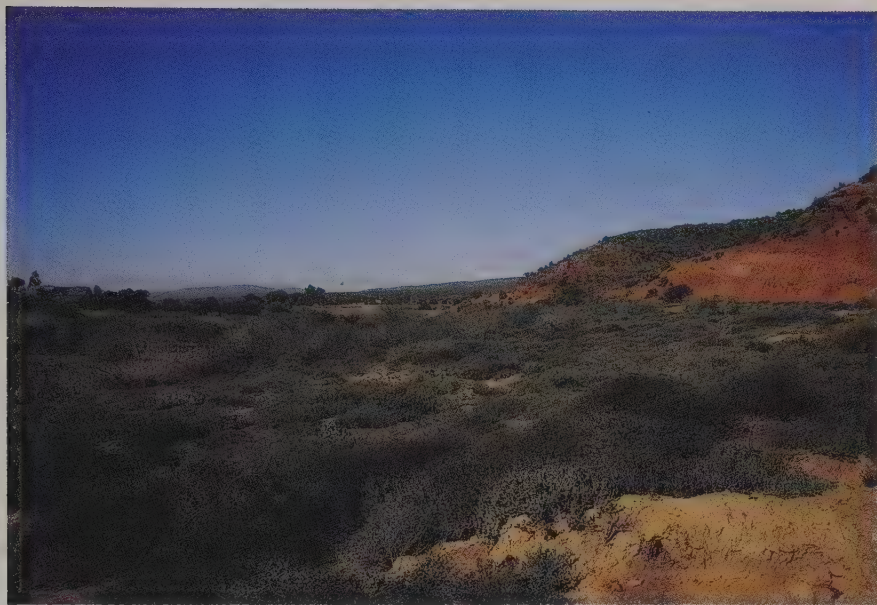


*Plate 5.* Klein Alexandershoek, west of Clanwilliam in an area of Macchia (Fynbos) (Acocks Veld Type 69).



*Plate 6.* Tierberg, Prince Albert, in an area of Karroid Broken Veld (Acocks Veld Type 26) in the southern Great Karoo.





*Plate 7.* Onverwacht, Oudtshoorn, in an area of Karroid Broken Veld (Acocks Veld Type 26) in the Little Karoo.



*Plate 8.* Hilton, Grahamstown district, in an area of False Karroid Broken Veld (Acocks Veld Type 37) in the southeastern Nama Karoo.



Plate 9. Female *Ceramius nigripennis* filling her crop with water while standing on the water surface. Actual length of female 15 mm.



Plate 10. Aggregation of *Ceramius socius* on wet sand near water's edge, females collecting water. Actual length of females 13.5 mm.





Plate 11. *Ceramius lichtensteinii* female with mud pellet held between mandibles, at a typical erect nest entrance turret. Actual length of wasp 19 mm.





Plate 12. *Allocoelia capensis* (Chrysididae: Allocoeliini). Actual length of wasp 12.5 mm.



Plate 13. A stamen carpet flower, *Drosanthemum* sp., being visited by *Quartinioides* sp. I. Actual length of wasp 4 mm.



Plate 14. A central cone flower, *Stoeberia* sp., being visited by *Quartinioides laeta*. Actual length of wasp 4 mm.



*Plate 15. A cup flower, Herrea sp.*





Plate 16. *Ceramius braunsi* visiting *Arctotis laevis* (Arctoteae), a ligulate capitulum. Actual length of wasp 17 mm.



Plate 17. *Ceramius braunsi* visiting *Athanasia trifurcata* (Anthemideae), a compound, nonligulate capitulum. Actual length of wasp 17 mm.



Plate 18. *Ceramius chypeatus* withdrawing from a flower of *Aspalathus spinescens* (Papilionaceae: Crotalarieae). Actual length of wasp 16 mm.





Plate 19. *Wahlenbergia pilosa* (Campanulaceae).



Plate 20. *Wahlenbergia prostrata* (Campanulaceae) being visited by *Quartinioides* sp. M, dorsal surface toward center of flower. Actual length of wasp 4 mm.



Plate 21. *Wahlenbergia annularis* (Campanulaceae) being visited by *Capicola* sp. C, ventral surface toward center of flower. Actual length of bee 9 mm.



Plate 22. *Aptosimum procumbens* (Scrophulariaceae).



Plate 23. *Aptosimum procumbens* (Scrophulariaceae).





Plate 24. *Peliostomum virgatum* (Scrophulariaceae).



*Plate 25.* Grootfontein, eastern Nama Karoo, showing two plots, one grazed only in winter and the other only in summer.

## Method of excavation

In Nest Types 1A, 2, and 3, nest builders carry water for use in construction in the crop. On arrival at the nest, the water is regurgitated and worked into the soil with the mandibles to form mud. The spoils of excavation are removed with the mandibles in the form of mud pellets, which are either discarded or used for the construction of a turret or for the construction of cells.

In Nest Types 1B and 6 the burrow is excavated in friable soil and water is not used. Different methods of extraction of the spoils of excavation are employed. A Type 1B nester, as exemplified by *R. angulata* and *R. maculata*, excavating a vertical burrow, removes sand from the nest held between the underside of the head and the prosternum, the genae being fringed with ammochaetae. A Type 6 nester, as exemplified by *Celonites latitarsis*, excavating a sloping burrow, rakes sand out with widely expanded tarsomeres.

The possession of ammochaetae fringing the genae is a generic character for *Rolandia* (Snelling 1986). It is therefore expected that all members of the genus excavate their nests in a similar manner. The only other vespid genus recorded as having a psammophore for the removal of the spoils of excavation is *Pterochilus* (Eumeninae) (Bohart 1940), for which nesting in vertical burrows in friable soil by two species has been described (Isely 1914 and Evans 1956). *Pseudepipona herrichi* (Saussure) (Eumeninae) removes sand particles with the mandibles one at a time (Spooner 1934). Sand raking by *C. latitarsis* is probably unusual for *Celonites*. Ten other Afro-tropical species of *Celonites* examined by us do not have widely expanded tarsomeres suitable for raking (Gess and Gess 1992). Indeed sand raking seems to be unusual not only for masarines but for vespids as a whole.

Not only are the substrate and the method of excavation of the burrows of Nest Type 6 very different in nature from those of Nest Type 3 but, just as important, the nature of and method of construction of the cells also differ in these two nest types. Whereas the earthen cells of Nest Type 3 are constructed from soil quarried within the burrow and bonded with water, those of Nest Type 6 are constructed from soil quarried at some distance from the burrow and bonded not with water but most probably with nectar. The method of construction and nature of the earthen cells of Nest Type 6 as exemplified by *C. latitarsis* in no way differ from these features of Nest Type 5 as exemplified by *C. wahlenbergiae*, nesting in



pre-existing burrows, and of Nest Type 4 as exemplified by the aerial-nesting *Celonites* species.

### Evolutionary sequence

A possible evolutionary sequence is discernible within the Masarinae from excavated burrows with excavated cells only (Nest Type 1) through excavated burrows with constructed earthen cells within excavated cells with earth for construction being derived from within the burrow (Nest Type 3) to the presumably more advanced construction of aerial earthen cells (Nest Type 4) (discussed in Gess and Gess 1980).

In the Sphecoidea and the Pompilidae nesting in friable soil without the use of water is considered to be primitive and nesting in nonfriable soil with the use of water derived. In the Masarinae and indeed in the Vespidae as a whole, however, nesting in friable soil without the use of water is seen as derived from nesting in nonfriable soil with the use of water (Gess and Gess 1992). Thus Nest Type 1B is seen as an offshoot from Nest Type 1A and is not considered to be part of the main evolutionary trend discernible within the Masarinae.

A further possible sequence, within the genus *Celonites*, has been suggested (Gess and Gess 1992); that is, a return to the ground from aerial constructed cells (Nest Type 4) through constructed cells in pre-existing cavities in the ground (Nest Type 5) to self-excavated burrows with constructed cells within excavated cells with earth for construction being mined outside the burrow (Nest Type 6). This second sequence is based on the method of construction of Nest Type 6: notably the sand-raking behavior with the consequent possession of sand-rakes as yet not recorded for any other masarines; soil for cell construction being obtained from a site at some distance from the nest not from within the nest; and the bonding agent being nectar, as used in Nest Types 4 and 5, not water, as is used in Nest Type 2.

Nest Type 7, in which self-generated silk is used for bonding, is distinct and is possibly derived from a vertical burrow excavated in stable friable soil without the use of a bonding agent.

Until such time as the nesting biology is known for a wide spread of species within all the genera, it will be premature to use nest characters in a cladistic analysis of the Masarinae. When Carpenter's proposed phylogeny of the Masarinae (Figs. 2, 3, and 4) together with the present

knowledge of nesting are considered, however, some comments can be made. Ground nesting together with the construction of an earthen turret as presently known for the *Paragia*, *Ceramius*, *Trimeria*, and *Jugurtia* lines can be derived directly from a common ancestor shared with the Eumeninae and most probably the Euparagiinae. A change to nesting in friable soil without the construction of an earthen turret has occurred more than once. The construction of aerial earthen cells, Nest Type 4, has evolved independently at least three times, once in the Gayellini and twice in the Masarini, in the *Pseudomasaris* and *Celonites* lines. Similarly the use of nectar instead of water as a bonding agent has evolved independently several times. Whether or not the use of silk produced by glands associated with the mouth is restricted to the *Quartinia* line and the choice of vertically presented ground to *Masarina* remains to be established.

# Associates

The associates of pollen wasps considered here are those arachnids and insects which are ectoparasites, endoparasites, "parasites" in nests, scavengers in cells, nest usurpers, and predators.

Masarine nests, when unattended, are open to intruders for, unlike many sphecoid wasps, masarines do not close their nests when leaving them. Females and those males which practice nest guarding do, when present in or near their nests, attempt to drive off intruders. They are, however, ill equipped for defensive action and are ineffectual against a persistent intruder.

The construction of a curved entrance turret, as practiced by many ground-nesting species, may offer some sort of protection. Certainly it effectively conceals the nest from some intruders, such as some bombyliid flies which are known to seek host nests in flight and to oviposit into a dark hole (Evans and Eberhard 1970; Linsley et al. 1980).

## *Ectoparasites*

### Acarina

Mites (Acarina) associated with adult pollen wasps have been recorded only for *Ceramius* species (Richards 1962; Gess 1965 and 1968). In the present study an examination of all the southern African genera of masarines revealed an association of mites with *Ceramius* alone. The presence of a pair of acarinaria positioned laterally on the metanotum of *C. caffer* and *C. metanotalis* was noted by Richards (1962) and of *C. rex* by Fred Gess (1965) (Fig. 47). In the specimens examined by Richards only

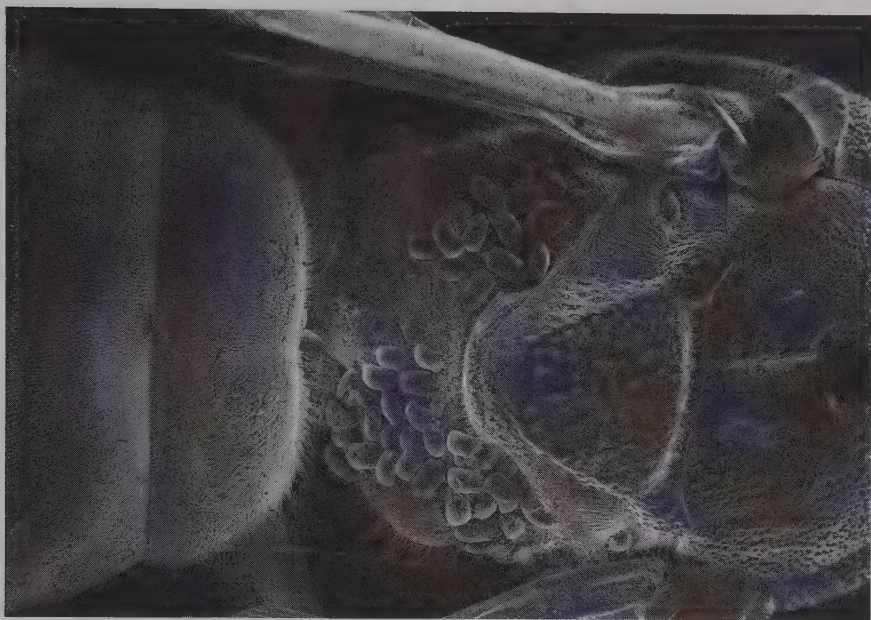


Figure 46. Hypopi of a winterschmitiid mite on an adult female *Ceramius nigripennis*, a species which does not have acarinarium ( $\times 18$ ).

the acarinarium of *C. caffer* contained mites, however, Fred observed mites in the acarinarium of all three species. In addition he noted that a female of *C. richardsi* which, like the rest of the *Ceramius* species, lacks acarinarium carried mites on the axillae and in the lateral depressions of the metanotum. He (Gess 1968) noted, in addition, mites similarly located on *C. cericeriformis* and *C. nigripennis* (Fig. 46). For the present study Fred examined 2,232 individuals, representing 18 of the 19 species of southern African *Ceramius* (Table 8). In this sample he found mites on all species of groups 3 and 6, all of which provision with composite pollen, but none on the species of groups 5 and 8 or on *C. beyeri*, the only species of Group 4 available, all of which provision with mesem pollen. The division on the basis of flower family visited is not clear-cut, however, as the two species of Group 2A, both of which provision with mesem pollen, bore mites. Similarly, the two species of Group 2B, both of which provision with





Figure 47. Hypopi of a winterschmitiid mite in one of the pair of acarinaria of an adult female *Ceramius rex* ( $\times 90$ ).

papilionate pollen, bore mites but none were found on the closely allied *C. micheneri*, which also provisions with papilionate pollen.

The mites were all hypopi (= heteromorphic deutonymphs) of the family Winterschmitiidae (= Saproglyphidae). A species of *Zethovidia* was obtained from adult females of groups 2, 3, and 6 and a species of *Kenethiella* only from adult females of Group 3.

Winterschmitiid mites are cosmopolitan and are richly represented in temperate or tropical zones of both hemispheres (Mostafa 1970). Some are free-living on dead, decaying organic material, but the majority are insect associates living in the galleries of bark beetles and in the nests of solitary bees and wasps (Mostafa 1970). The association with bees and wasps may be parasitic or symbiotic, the mites either sucking blood from but not harming the wasp prepupae and pupae or feeding on organic debris in the cells (Krombein 1967). The developmental stages of these mites consist of the egg, larval, nymphal, and adult stages ordinarily found in other mite



groups. The larva, protonymph, tritonymph, and adult have functional mouthparts but the hypopus (deutonymph) is a resting stage which lacks mouthparts and has a suctorial plate ventrally on the opisthosoma (Mostafa 1970). Hypopi of many winterschmitiid mites are phoretic on insects (Krantz 1978) to which they attach themselves with their suctorial plates.

Many winterschmitiid mites are related in their mode of living to the insects with which they are associated (Woolley 1989). Some have developed a very complex symbiotic relationship with solitary vespoids (Krombein 1961). Krombein's account of the life history of winterschmitiids associated with vespoids is based on studies of the mites *Vespacarus* and *Monobiacarus*. The rhythmic pulsation of the wasp's abdomen during movement of the egg from the oviduct prior to oviposition may be the signal for as many as 20 hypopi to leave the wasp's body and drop off in the cell. The transformation of the mites to the tritonymphal and adult stages takes place in the interval of a few days between oviposition by the wasp and completion of feeding by the wasp larvae. The adults are on the wasp larva as it begins to spin, and they are enclosed in the finished cocoon. They begin to feed on the wasp larva as soon as it has voided the meconium and has assumed the quiescent form. In heavy infestations by winterschmitiid mites the resting wasp larva is literally peppered with tiny black feeding punctures. However, Krombein never observed that this feeding was injurious to the wasp.

The engorged adult female mite ceases feeding and begins to lay eggs as soon as the wasp transforms to the pupal stage. The mites' larval and protonymphal stages are passed on the pupa, over which they wander more or less freely. Most of the mites are in the protonymphal stage when the adult wasp is ready to shed the pupal exuviae. As eclosion draws near, the mites cluster on the venter of the wasp around the mouthparts and legs. They are shed along with the pupal exuviae and in a brief time transform to the deutonymphal state (hypopus). Those of *Vespacarus* leave the pupal exuviae and clamber onto the tip of the wasp's abdomen and crawl forward until they reach the apical margin of the depressed acarinarium. They then turn around and back into the acarinarium.

It seems likely that the winterschmitiid mites associated with *Ceramius* species will be found to have a similar life cycle. However, the hypopal stage appears to be reached earlier in the life cycle of these wasps, hypopi having been found on last-instar resting larvae (prepupae) of *C. nigripennis* of Group 3 and *C. rex* of Group 6.

Table 8. Incidence of adult carriage of mites by southern African *Ceramius* species.

<i>Ceramius</i> species	Present study				Richards 1962				Gess 1965 + 1968			
	No. examined		No. with mites		No. examined		No. with mites		No. examined		No. with mites	
	F	M	F	M	F	M	F	M	F	M	F	M
Group 2A												
<i>cerceriformis</i>	88	58	51	8					30	9	19	1
<i>peringueyi</i>	22	2	1	1								
Group 2B												
<i>chypeatus</i>	144	31	24	1								
<i>richardsi</i>	7	1	5	0					6	2	4	0
Group uncertain												
<i>micheneri</i>	20	45	0	0								
Group 3												
<i>braunsi</i>	133	10	23	0								
<i>jacoti</i>	28	6	1	3								
<i>nigripennis</i>	160	46	136	2					64		21	
<i>toriger</i>	70	36	64	0								

[illegible]

## *Endoparasites*

### Strepsiptera

The order Strepsiptera comprises a small number of very anomalous insects, the larvae of which are endoparasitic. They are sometimes classified as Coleoptera (Crowson 1981). The majority of females remain all their lives in a puparium which protrudes slightly from the body of the host. The adults are termed "stylops" and an insect bearing these parasites is said to be "stylopized." They have been recorded from Thysanura, Blattodea, Mantodea, Orthoptera, Hemiptera, Diptera, and aculeate Hymenoptera (Kathirithamby 1991).

In examining in excess of 5,000 Afrotropical pollen wasps, Fred Gess (pers. comm.) found none which had been stylopized. The Australian *Paragia* (*P.*) *decipiens* is in fact the only masarine which has been recorded as being stylopized. Records were given by Richards (1962) and by Naumann and Cardale (1987), and in addition specimens of *P. decipiens* in the South African Museum were noted by Fred (pers. comm.) to be stylopized. In their sample of *Paragia* (*P.*) *decipiens* Naumann and Cardale found that 25 percent ( $n = 24$ ) of adult females and 13 percent ( $n = 54$ ) of adult males were stylopized. Riek (1970) gave the identity of the strepsipteran associated with *P. decipiens* as a species of *Paragioxenos* of the family Stylopidae.

Richards (1962) observed that, of the 13 male and 6 female parasites he recorded, the males were beneath tergite 3 and the females beneath tergite 4 and that a parasitized female *Paragia* acquires male characters. A male is less altered but the tubercle of sternite 2 is reduced.

### *"Parasites" in nests*

"Parasites" recorded from masarine nests are species of Mutillidae, Chrysididae, ?Chalcididae, Gasteruptiidae, Meloidae, and Bombyliidae.

### Mutillidae

Mutillids, commonly called velvet ants, are larval ectoparasitoids of terrestrial immatures of other insects—fully fed larvae or pupae of a wide variety of bees and wasps within cells and/or cocoons; the puparia of some flies; the pupae of some moths; the pupae of some beetles; and the oothecae of

cockroaches having been recorded (Brothers 1989). Typically the female mutillid penetrates the cocoon or puparium with its ovipositor and deposits an egg or eggs either on the host or the inner wall of the cocoon (Mickel 1928). Up to four individuals are known to develop on a single host (Brothers 1984). Any one species of mutillid is not necessarily limited to a single species or genus of host. Rather, they appear to be associated with a particular ecological niche and to attack suitable host species found within that niche. For example, *Dasylabroides caffer* (Kohl) has been reared from cocoons of a masarine wasp *Ceramius lichtensteinii* (Gess and Gess 1980) and also from cocoons of two sphecids wasps, *Ammophila ferrugineipes* Lepeletier and *Ammophila insignis* Smith (Weaving, pers. comm.). Additional records of mutillid/masarine associations are *Stenomutilla argentata* (Vill.) as a probable "parasite" of *Masaris vespiformis* (Ferton 1920) and *Photopsis* sp. as a parasite of *Pseudomasaris edwardsii* (Hicks 1929).

## Chrysididae

All species of chrysidids, commonly called cuckoo wasps, are "parasitic." The nature of the host is practically a subfamilial character in Chrysididae. Thus, Amiseginae and Loboscelidiinae attack stick insect eggs, Cleptinae sawfly pupae, and Chrysidinae (except *Praestochrysis*) aculeate wasp and bee larvae (Kimsey and Bohart 1990). Some of the Chrysidinae monitor the nests of their hosts and will enter and oviposit at the stage when a cell has received an egg and provision; others break into closed cells or dig through closed entrances in order to oviposit (Evans and Eberhard 1970). In the former case the egg hatches before or after that of the host and, having found the egg or small larva of the host, the chrysidine destroys it and consumes the provision (Krombein 1967; Evans and Eberhard 1970). In the latter there is reason to believe that it may be the fully grown larva and not the provision which is consumed (Evans and Eberhard 1970).

Kimsey and Bohart (1990) record the chrysidine genera *Allocoelia* (Allocoeliini), *Chrysis* (Chrysidini), *Chrysurissa* (Chrysidini), and *Spintharina* (Chrysidini) to be associated with masarines.

*Allocoelia* of the monogeneric tribe Allocoeliini occurs in southern Africa, specifically in Namibia, Zimbabwe, and South Africa. Suggestive evidence for an association between *Allocoelia* and pollen wasps is the fact that of the nine *Allocoelia* species we have found seven in association with pollen wasp nests (Table 9) (Gess 1973; Gess and Gess 1980 and unpub-



Table 9. *Allocoelia* species associated with masarine nests.

<i>Allocoelia</i> species	Masarine species	Locality
<i>bidens</i> Edney	<i>Jugurtia confusa</i>	Hilton, Grahamstown
<i>capensis</i> (F. Smith)	<i>Ceramius lichtensteinii</i>	Clifton, Grahamstown
	<i>Ceramius cerceriformis</i> (as <i>C. schultzei</i> )	? Willowmore (Brauns 1910) ? Willowmore (Brauns 1913)
<i>glabra</i> Edney	<i>Masarina familiaris</i>	11 km W Clanwilliam
<i>latinota</i> Edney	<i>Ceramius capicola</i>	Strowan, Grahamstown
	<i>Ceramius lichtensteinii</i>	Tierberg, Prince Albert
<i>minor</i> Mocsary	<i>Ceramius capicola</i>	Strowan, Grahamstown
	<i>Ceramius clypeatus</i>	Clanwilliam Dam
<i>mocsaryi</i> (Brauns)	<i>Quartinia vagepunctata</i>	15 km N Nieuwoudtville
<i>quinquidens</i> Edney	<i>Masarina familiaris</i>	11 km W Clanwilliam
	<i>Masarina strucki</i>	Goegab, Springbok Kamieskroon

Source: Gess and Gess records except where otherwise indicated.

lished field notes) and have seen them monitoring nests which are being worked upon. Definite evidence is that one of these, *A. capensis* (F. Smith) (Plate 12), has been reared from cells of *Ceramius lichtensteinii* (Brauns 1910). The remaining two species occur within the distribution range of the masarines in the southwestern Cape, and it seems probable that they will also be found to be associated with these wasps.

Two genera of Chrysidini, *Chrysurrissa* and *Spintharina*, like *Allocoelia* seem to be closely associated with the Masarinae. *Chrysurrissa densa* (Cresson), the only described species of *Chrysurrissa*, occurs in western North America. It has been reared from the nests of *Pseudomasaris* species, specifically *P. vespoides* and *P. edwardsii* (as *Chrysis densa*, Hicks 1927 and 1929 respectively), *P. zonalis* (as *Chrysura densa*, Parker 1967), and *P. occidentalis* (as *Chrysis densa*, Hungerford 1937).

Kimsey and Bohart (1990) list 26 species of *Spintharina*, 14 Palearctic and 12 Afrotropical, and note that most inhabit arid zones. In the Palearctic Region *S. versicolor* (Spinola) is known as a parasite of *Celonites* sp. (Linsenmaier 1959). In the Afrotropical Region *S. arnoldi* (Brauns) was reared from a putative nest of *Celonites promontorii* (Gess and Gess, unpub-

lished), and *S. bispinosa* Mocsary (as *Sintharis* [sic] *bispinosa*) has been reared from cells of *Celonites andrei* (Brauns 1913) and recorded as present in a nesting aggregation of *Jugurtia confusa* (Gess and Gess, unpublished fieldnotes).

Four species of *Chrysis* have been recorded as parasites of masarines: *C. tingitana* Bischoff of an unidentified masarine (Linsenmaier 1959); *C. emarginatula* Spinola of *Ceramius lusitanicus* (Ferton 1901); *C. splendidula* Rossi (as *C. versicolor* Spinola) of *Celonites abbreviatus* (as *C. apiformis*) (Berland and Bernard 1938); and *C. atracomitita* Linsenmaier of *Quartinia canariensis* (Gusenleitner 1990a). Species of the large and widely distributed genus *Chrysis* of about 1,000 species have otherwise been recorded as "parasites" of a wide range of wasps and bees of the families Sphecidae, Larridae, Philanthidae, Vespidae: Eumeninae, Megachilidae, and Anthophoridae (Kimsey and Bohart 1990).

### ?Chalcididae

An unidentified chalcid has been recorded from the nest of *Pseudomasaris edwardsii* (Hicks 1929).

### Gasteruptiidae

Gasteruptiids oviposit into the nests of sphecoids, vespids, and bees, where the larva feeds on the egg or larva and provision of the host (Gauld and Bolton 1988).

*Carinafoenus* sp. has been recorded from the nesting area of *Paragia* (*P.*) *tricolor* and gasteruptiid larvae were found in three cells of this wasp (Houston 1984). Houston concluded that the gasteruptiid *Carinafoenus* sp. evidently develops on the provision of *Paragia*, probably after the destruction of its eggs. Several observations have been made of another gasteruptiid, *Hyptiogaster* sp., entering nests of *Paragia* (*P.*) *decipiens* (Naumann and Cardale 1987).

### Meloidae

As far as is known, all meloids show hypermetamorphosis, with an egg, a very active first-instar larva (triungulin), three fleshy grublike feeding stages (caraboid and two scarabaeoid), two nonfeeding stages (coarctate (pseudo-pupal) and scolytoid), and a pupa (Clausen 1940). The triungulins are

broadly divisible into two types, nonphoretic and phoretic (Crowson 1981; MacSwain 1956). A nonphoretic triungulin has "running" legs and finds its own way to its host's nest or egg burrow, whereas a phoretic triungulin has "clamp-like" legs with which to attach itself to its host, which then carries it to its nest. The adults are flower feeders, and the larvae of in excess of 76 species feed on acridid eggs (Greathead 1963) and in excess of 34 species on the provision laid in by bees, Megachilidae, Andrenidae, and Anthophoridae (Xylocopinae) (Krombein et al. 1979; Watmough 1974; Gess 1981). The larvae of a few species are known to feed on the larval provision and larvae of aculeate wasps, one larrid (Fabre 1943), two eumenines (Gess and Gess 1976a, 1991b), and one masarine, *Ceramius lichtensteinii* (Brauns 1910; Gess and Gess 1980). Brauns found the coarctate larvae or pupae ("Puppen") of a meloid in the masarine wasp's cells but was unable to identify them as he was unable to rear them through to the adult stage. We found two adult specimens of *Ceroctis groendali* (Billberg) (Lyttninae: Mylabrini) and six meloid larvae in various stages of development in cells of *C. lichtensteinii* (Table 10). Though we attempted to rear these larvae, none came through to the adult stage so we could not prove their identity. It is, nevertheless, believed that they were conspecific with the adults.

The triungulin larvae from cells of *C. lichtensteinii* have "running" legs. Their association with their masarine host is consequently not brought about by chance collection of phoretic triungulins waiting in flowers for visiting bees.

The fourth-instar larva of some species is known to migrate and to prepare a pupal cell apart from the host's nest cell or egg burrow (MacSwain

Table 10. Contents of cells of *Ceramius lichtensteinii* in which four meloid larvae were found.

Meloid larval stage	Masarine egg or larval stage	State of masarine pollen loaf
Triungulin, moulted and died	Egg near hatching	Being fed upon
Probably first scarabaeoid, fed and moulted three times to coarctate resting stage	Large pre-spinning larva, killed and eaten	Finished
Second scarabaeoid, died	None	Being fed upon
Second scarabaeoid, died	Small, dead	Being fed upon

1956), but the complete development of the beetle after the larva has reached a cell of its masarine host takes place within that cell. Migration is probably precluded by the nonfriable nature of the cell wall and of the soil in which the masarine nests are constructed.

We established that the meloid larvae feed upon both the provision and the larva of the masarine.

## Bombyliidae

The majority of bombyliids are in the larval stage "parasitic" on the eggs, larvae, or pupae of other insects (Bowden 1980) and are well known from the nests of wasps (Evans and Eberhard 1970) and bees (Linsley et al. 1980). It is therefore surprising that no bombyliids have been reared from the nests of masarines, however, several observations have been made of *Anthrax* sp. entering nests of *Paragia* (*P.*) *decipiens* (Naumann and Cardale 1987).

## Scavengers in cells

### Acarina

Eggs, nymphs, and adults of a mite, *Tyrolichus casei* Oudemans (Acaridae), a pest of stored products, were found in a cell of *Paragia* (*P.*) *tricolor* (Houston 1984). No host immature was present.

## Nest usurpers

### Megachilidae

In southern Africa ground-nesting masarines are subject to usurpation of nests by megachilid bees. We have recorded *Megachile aliciae* Cockerell from nests of *Ceramius nigripennis* in the Springbok district, Namaqualand (Gess and Gess 1986), and of *Ceramius braunsi* in the Clanwilliam district, Olifants River Valley (Gess and Gess 1990); an undetermined megachilid from nests of *Ceramius jacoti* in the Oudtshoorn district, Little Karoo (Gess and Gess 1988b); and a species of *Hoplitis* from nests of *Masarina familiaris* in the Clanwilliam district (Gess and Gess 1988a). *M. aliciae* is not restricted to usurping the nests of masarines, having been recorded by us usurping nests of *Parachilus insignis* (Saussure) (Eumeninae) in the

Grahamstown district, eastern Cape (Gess and Gess 1976a), and of *Paravespa mima* Giordani Soika (Eumeninae) in the Prince Albert district, southern Great Karoo (Gess and Gess 1988c).

It was the activity of the bee *M. aliciae* which originally drew our attention to the presence of a *C. nigripennis* nesting aggregation. Several of these bees were harassing the wasps, which had clearly just started nesting as all were constructing turrets. Three days later I investigated 15 turreted nests and of these three contained *M. aliciae* cells. In two of these nests the bee had made use of the cell from which the wasp had emerged. In both instances it was clear that the wasp had been evicted, as the bee had sealed the main shaft a short way below ground level. The third nest was newly excavated and contained a single newly constructed-mud cell in which the bee had constructed her own cell. The bee had not yet sealed her cell and was found in the nest. In addition I investigated two nests from which no wasp had yet emerged in the present season. Both contained *M. aliciae* cells. Four of eight nests of *C. braunsi* which I investigated contained a petal cell. All of the nests were new and one-celled. Two were closed with a final bee seal, but in each of the other two, in which the petal cells were still being constructed, I found a female *M. aliciae*.

The bee constructs its flask-shaped petal cell within the masarine's cell in such a way that it entirely fills the latter (Gess and Gess 1986, Fig. 16, 1990, Fig. 12). The petal cells from *C. nigripennis* nests were all constructed from lengths cut from the orange "petals" of the Namaqualand Daisy, *Dimorphotheca sinuata* (Asteraceae), and three of those from *C. braunsi* nests from the pink petals of a species of *Pelargonium* (Geraniaceae). The "petal" pieces are carried to the nest cut-end first. They are arranged in such a way that a round-bottomed "flask" is constructed with the "petals" running vertically and tucked under at the bottom.

The provision is syrupy. I examined pollen from provision, a mixture of pollen and nectar, from both sites and found that it was a mixture derived from two or more plant species. This I compared with pollen from plants flowering in the vicinity of the nests. One of the pollens matched that from a yellow-flowered species of *Homeria* (Iridaceae), another was of the spiny composite type, and three others were probably from "mesems." Pollen from *D. sinuata* and the *Pelargonium* species did not match any of the pollen derived from the bee's cells. Pollen for provision was therefore collected from different plants from those from which nesting materials were taken.



After provisioning and oviposition have taken place, the bee seals the cell using shorter pieces of "petal" laid cross-wise across the mouth of the petal cell. The ends of these shorter petals are curved upward into the mouth of the wasp's mud cell, which is then sealed with a mud plug, concave above and with a smooth surface. Sealed mud cells containing bee cells are readily distinguishable from sealed cells of *C. nigripennis*, the mud plugs of which are convex above and with the surface left rough (Fig. 48).

The bee constructs a final closure in the main shaft about 5 mm below the ground surface (Fig. 49). This closure consists of a short length of "petal" laid across the shaft followed by a layer of mud, concave above with the surface smoothed.

The megachilid which had invaded a *C. jacoti* nest had constructed a leaf cell within the nest.



Figure 48. Three earthen cells of *Ceramius nigripennis*: convex seal of *C. nigripennis* (top); open cell (bottom left); concave seal of *Megachile aliciae* (bottom right).



Figure 49. Vertical plan of nest of *Ceramius nigripennis* usurped by *Megachile aliciae*, showing position of final bee seal (arrow).

I observed a species of *Hoplitis* in attendance at two nests of *M. familiaris*. One nest was an old two-celled nest which lacked a turret, but the other was a newly constructed four-celled nest which was being attended by its wasp builder in addition to the bee usurper.

The wasp cells utilized by the bee had been widened by the latter prior to the construction of its petal cells. The petals utilized were those of the purple-flowered *Cyanella hyacinthoides* (Amaryllidaceae) growing in the vicinity. After a petal cell had been sealed with pieces of petal, the excavated cell had been sealed with compacted soil.

Pollen from the provision was a mixture of pollen and nectar derived from three or more plant species. I examined pollen from *C. hyacinthoides* but it did not match any of the pollen derived from the bee's cells. Pollen for provision was therefore collected from different plants from that from which nesting materials were taken.

### *Predators*

There are no records of predators that prey specifically on masarines. Masarines, however, have been listed as prey of two sphecoids that provi-

sion with mixed hymenopteran prey. *Ceramius capicola* has been recorded as prey of *Palarus latifrons* Kohl (Larridae) in southern Africa (Brauns 1911) and two *Pseudomasaris* species, *P. edwardsii* and *P. zonalis*, have been recorded as prey of *Philanthus zebratus* (Cresson) (Philanthidae) in Wyoming, U.S.A. (Evans 1970; Evans and O'Neill 1988).

Although not recorded, it is highly likely that birds, robber flies (Asilidae), assassin bugs (Reduviidae), mantids (Mantodea), and crab spiders (Thomisidae), which prey upon flower-visiting insects, include masarines in their captures.

It seems likely that the fully grown larvae and the stored pollen and nectar provision are a food resource for some small mammals. Certainly we have found empty, broken earthen cells of *Ceramius* species scattered on the ground in nest aggregation sites which showed signs of the diggings of some small animal (Gess and Gess, unpublished fieldnotes).

## Pollen Wasps as Potential Pollinators

Studies of aculeate Hymenoptera as pollinators have been concerned in the main with bees. General works on pollination—such as those by Percival (1969), Proctor and Yeo (1973), A. J. Richards (1978), Faegri and van der Pijl (1979), Jones and Little (1983), Real (1983), and Barth (1985)—have few references to flower visiting by any aculeate wasps. Masarines are mentioned only in Proctor and Yeo (pp. 367–368), Jones and Little (in chap. 6 by Simpson and Neff, p. 148), and Barth (pp. 33 and 61). Vogel (1954) in his study of the pollinators of the southern African flora surprisingly makes no mention of masarines. However, Whitehead and coauthors, in Rebelo's (1987) preliminary synthesis of pollination biology in the Cape flora, state that masarines "are probably important floral visitors in southern Africa," but they give no indication of masarine/flower associations even though flower-visiting records were available to them in Gess (1968 and 1973) and Gess and Gess (1980 and 1986).

In his world revision of the Masarinae, O. W. Richards (1962, pp. 32–34) reviewed the literature on flower visiting by these wasps and concluded that "higher Masarids are so closely attached to particular kinds of flowers that the subject cannot be omitted from any serious study of the group though our knowledge is still very incomplete and in some respects inaccurate. It may well be possible in the future to relate the structure of some of the genera to that of the flowers they visit and to the methods which they use in exploiting them." This conclusion is not directly supported by

Richards but appears to be based on Cooper's (1952) contention that most *Pseudomasaris* species for which flower associations were known were essentially oligolectic and on his own statement based on the scant records available to him that in the *Quartinia* group nearly all species favor Asteraceae (as Compositae).

Torchio (1974) investigated the potential of *Pseudomasaris vespoides* as a pollinator of *Penstemon* (Scrophulariaceae) and showed that the wasp/flower fit and wasp behavior do support such a potential relationship with some violet-flowered *Penstemon* species. Blue-flowered species he considered to be bee-pollinated and red-flowered species to be bird-pollinated.

In a study of the ethology of *Rolandia angulata* we (Gess et al. 1995) evaluated the association of this pollen wasp with *Goodenia* (Goodeniaceae) flowers, their source of pollen and nectar. We concluded that the association with *Goodenia pinnaatifida*, at least, is mutually beneficial. Indeed we suggested that in some areas, at some times, *R. angulata* may be the most important potential pollinator of this plant.

Our preliminary investigation of flower visiting by pollen wasps in southern Africa (Gess and Gess 1989) demonstrated high-percentage associations of pollen wasps with Asteraceae and Aizoaceae and in addition marked but lower-percentage associations with Papilionaceae, Campanulaceae, and Scrophulariaceae. We also noted a high incidence of oligolecty, a measure of the importance of the plants to the pollen wasps. It is not, however, necessarily a measure of the importance of the pollen wasps as pollinators of the flowers which they visit. This chapter attempts to evaluate the potential of pollen wasps as pollinators and their possible importance as such to the plants with which they are associated.

For a flower to be pollinated by a visitor, that visitor must receive pollen from a flower in such a position that when it enters a conspecific flower with a receptive stigma some of that pollen is transferred to the stigma. For this transfer to be successfully achieved, the visitor must in all but "mess"-pollinated flowers follow a regular pattern of behavior and "fit" the flower. In our 1989 paper we gave examples of pollen wasps which do fulfil these requirements.

The present chapter explores in greater depth the flowers visited by pollen wasps and attempts to evaluate comparatively their insect visitors as potential pollinators. The flowers will be considered in the context of the groups to which they belong. First, however, it is necessary to



preface these accounts with a consideration of some of the requirements of pollinators.

Clearly the assumption of Whitehead et al. (1987) that the "nine families of bees occurring in southern Africa are all *important pollinators* of the local flora, *since they require pollen* as a protein source for their progeny" (emphasis added) is illogical. It is essential that a pollinator should transport pollen, but the potential of an insect as a pollinator cannot be judged by its pollen requirements. Pollen that is deliberately collected by pollen wasps and bees and stowed away for transport by ingestion into the crop (masarines and some colletids) or packed into external pollen-carrying structures (most bees) is not available for pollination. Pollination is brought about by free pollen, which adheres, usually accidentally, to the carrier, not by pollen collected for provisioning. Pollen which is free for pollination is just as likely to be collected and transferred by an insect collecting nectar as by an insect collecting pollen. Indeed this transfer is most frequently performed by insects seeking nectar rather than pollen (Kevan and Baker 1983). Cross-pollination requires movement between flowers. This is achieved if the nectar produced is enough to attract but not enough to satisfy (Kevan and Baker 1983).

If the insect positions itself randomly, the chance of pollen being successfully transferred will also be random and the chances of its pollinating the flower will be random. If, however, the insect positions itself regularly and this positioning is such that successful pollen transfer is brought about, then the chance of its pollinating the flower will be high.

Insect size in relation to flower size is of variable importance. As with regularity of behavior, good insect/flower fit generally increases in importance with an increase in flower complexity. Gullet flowers and campanulate flowers, for example, require a snug insect/flower fit. A relatively small insect is able to enter and leave these flowers successfully obtaining nectar and pollen for its own use without necessarily receiving a pollen load or coming into contact with the stigma. A relatively overlarge insect, on the other hand, is not able to enter these flowers, though if it has a long enough proboscis it may be able to rob a flower of nectar without receiving a pollen load or coming into contact with the stigma. For successful pollination of papilionate flowers, the size restraint is clearly not one of insect/flower fit in the sense of the insect fitting snugly into the flower but of its being of the correct size and weight to trip the mechanism which permits the release of the essential parts from the keel in which they are

enclosed. A flower visitor specializing in flowers of a particular taxon may, because of size differences between flowers of different species, even of the same genus, successfully pollinate some and yet fail to pollinate others. Such species therefore have a mutualistic relationship with some of the flowers they visit and yet their visits to other flowers are of benefit only to themselves.

Pollinators show varying degrees of dependability, and insect-pollinated flowers show varying degrees of specialization with respect to "acceptability" of insect visitors. One species of insect visiting only one species of flower, the ultimate in dependability, is the exception. Flower visitors which visit a small number of related plant species are clearly more dependable than visitors which visit a large number of unrelated plant species, as the probability of their choosing a particular species of flower is greater. Where only one of their preferred flower species occurs in an area where other plants not favored are in flower, they will clearly be expected and dependable visitors to that species. Such a plant may depend solely on the services of this one species of insect for pollination or it may be serviced by a guild of such specialists, which are themselves either related or not related. Plants of this type may even in addition be randomly serviced by generalist species. Indeed generalist flowers, pollinated randomly by a wide range of insects or at least a wide range of wasp and bee species, may be among those plants favored by specialist species. The evolutionary factors favoring specialist or generalist pollinators are not necessarily the same as those favoring specialist or generalist flowers (Kevan and Baker 1983).

Care must be taken not to confuse restriction to a single plant species with temporary fidelity. Some insect visitors, having found a plant species in flower which proves to be a good resource, show temporary fidelity to flowers of that species. When the rewards diminish, the visitor may transfer to flowers of an unrelated species, to which it then shows temporary fidelity. While working flowers of a particular species, it may be servicing them more efficiently than a more dependable visitor. It may or may not be reliable on a year-to-year basis, however, and is even less likely to be reliable on a locality-to-locality basis.

There follows an evaluation of pollen wasps as potential pollinators of the plants of the families most favored by them in southern Africa: the Aizoaceae (just Mesembryanthema), Asteraceae, Papilionaceae (just Crotonarieae, of the Cape Group), Campanulaceae and Scrophulariaceae. The

evaluations take into account the biology of the flowers and compare the pollen wasps and the other members of the flower-visiting guilds, taking into account pollen carriage, pattern of and regularity of behavior in or on flowers, flower fit, and dependability. The presentations for the Aizoaceae and Asteraceae are generalized. Those for the Crotalariaeae are by flower genus and demonstrate that a characteristic guild structure can be recognized at that level. Those for Campanulaceae and Scrophulariaceae are for flower genus and species, as there are marked differences in guild structure at the generic and specific levels.

### *Aizoaceae*

The family Aizoaceae has been variously delimited. In the present account the assessment of Bittrich and Hartmann (1988) is followed. The family is seen to consist of five subfamilies arranged in two groups: Aizooideae, Sesuvioideae, and Tetragonioideae form one group without a formal taxonomic rank and name; Rushioideae and Mesembryanthemoideae form the second group, named Mesembryanthema.

The non-Mesembryanthema are cosmopolitan in distribution. The distribution of Mesembryanthema is centered in southwestern Africa (Hartmann 1991). As already noted (Chapter 3), there is a striking similarity between the overall distribution and areas of diversity richness of the Afrotropical masarines (Fig. 7) and Mesembryanthema (Fig. 21).

In the western Cape, particularly north of the Olifants River Mountains, with a high species diversity of both Mesembryanthema and masarines, the peak of the flowering period for some species of Mesembryanthema is from late September to late October. This coincides with the peak of the flight period for masarines as a group. The peak flowering time of other species falls either earlier or later. Many of those species of Mesembryanthema flowering earlier have their peak flowering times coincident with the peak of the flight period of *Fidelia* (Fideliidae). Whitehead (1984) recorded three species which are restricted to Mesembryanthema for obtaining both pollen and nectar. The lists of insects collected on early-flowering Mesembryanthema in the Goegab Nature Reserve by Struck (1990) indicate that these species are patronized by, in addition to fideliids, a wide range of other bees, almost all generalists.

The Mesembryanthema are most strikingly separated from the other subfamilies by the possession of brightly colored petaloid staminodes.

Hartmann (1991) reviews the knowledge of their reproductive biology. She states that:

Most flowers are protandrous and open repeatedly by basal growth of the androecial elements. At the same time, the stigmata elongate, and later they spread. As a consequence, most flowers have a distinctive early male and later female phase. One of the most common patterns of development is that the stigmata (styles are very rare in *Mesembryanthema*) are at first shorter than the stamens. When the stamens wither, they collapse, and the elongating stigmas take a prominent place in the centre of the flower. At the same time the stigmas spread widely and present a conspicuously papillate surface which is also more intensively coloured than in the unripe green state.

Hartmann further states that "only a few data on the pollination of *Mesembryanthema* are available" and cites Vogel (1954), Gess and Gess (1989), and Liede (1990a, 1990b). To this should be added the preliminary comments and list of insect visitors to selected species in the Goegab Nature Reserve given by Struck (1990).

Vogel (1954) recognized clear divisions of form, including six forms suited to Hymenoptera and others to Lepidoptera. His divisions are represented and amended by Hartmann (1991). The forms suited to Hymenoptera—that is, the melittophilous forms—are characterized by an open presentation of large quantities of pollen in conjunction with hidden nectaries, diurnal opening of the flowers, and bright, shiny, petaloid staminodes. These forms can be summarized as follows:

1. Stamen carpet flowers (Fig. 50, Plate 13)

The open flower is rather flat and almost saucer-shaped, the petaloid staminodes are much longer than the stamens. In the male phase the center is completely filled by numerous stamens and an insect walking on a flower receives a coating of pollen ventrally. In the female phase the center of the flower is occupied by the spreading stigmas. As pollen is no longer available, it may well be that nectar production becomes important in this phase. It is assumed that pollen is transferred onto the stigmas from insects in search of nectar.

Stamen carpet flowers are widespread in the *Mesembryanthema*.

Genera included in the flower-visiting catalogues (Appendices 1 and 2) are: *Aridaria* subg. *Aridaria*, *Delosperma* (some species only),



*Figure 50.* Stamen carpet flower, longitudinal section.



*Figure 51.* Central cone flower, longitudinal section.



*Figure 52.* Cup flower, longitudinal section.



*Drosanthemum*, *Malephora*, *Leipoldtia*, *Mesembryanthemum*, and *Car-pobrotus*.

2. Central cone flowers (Fig. 51, Plate 14)

In these flowers there are two kinds of staminodes. The larger outer ones are petaloid and open out horizontally, and the inner ones surround the stamens in the form of a central cone. Differences in size determine the processes of pollen transfer.

2A. Small central cone flowers

These are small flowers (up to 20 mm in diameter) with low, central cones of stamens which, according to Vogel (1954) and Hartmann (1991), only permit a visiting insect to insert its proboscis into the cone. In the male phase the head of the insect makes contact with the pollen. To deliver the pollen in the female phase, the receptive parts of the stigmas must be placed in an equivalent position. This implies that the central cone is kept in its shape almost unaltered during the entire anthesis. The tips of the withering androecial elements curl up while the tips of the stigmas spread over them.

Genera included in the flower-visiting catalogues (Appendices 1 and 2) are: *Ruschia*, *Stoeberia*, *Mestoklema*, *Polymita*, *Psilocaulon*, *Delosperma* (some species only), *Prenia*, and *Sphalmanthus*.

2B. Large central cone flowers

These are large flowers (over 20 mm in diameter) which, according to Vogel (1954) and Hartmann (1991), have rather high, central cones, which the insects have to enter in order to reach the nectar.

Not represented in the catalogue.

3. Recess flowers

A recess or hidden cavity is developed in the center of these flowers, into which the visiting insects have to crawl in order to reach pollen or nectar. The insect when entering receives a coating of pollen all over. Delivery of pollen to the stigmas is left to chance, the probability of success being high. Morphologically, the recess is formed by a more or less well developed hypanthium, at the upper rim of which the nectary is placed. The petaloid staminodes spread out horizontally. The stigmas are reduced and are sometimes connate, forming a cushion.

Not represented in the catalogue.

4. Cup flowers (Fig. 52, Plate 15) [I have added this type, as it does not seem to be covered by the types described by Vogel 1954 and Hartmann 1991.]

In these flowers the receptacle is unusually wide. The petaloid staminodes are very numerous, in several series spreading in different planes. The stamens are at first inflexed and reach the stigmas, then erect and finally spreading, not forming a "carpet" but rather a loose "cup."

One genus is included in the flower-visiting catalogue (Appendices 1 and 2): *Herrea*.

When envisaging the behavior of visitors to their flower types, Vogel (1954) and Hartmann (1991) seem to have had in mind a "standard" bee.

In the present study I have established that in southern Africa 45 percent of pollen wasps for which flower-visiting records are available visit the flowers of Aizoaceae, principally of the group Mesembryanthema, to which the majority is probably restricted. Clearly those species which are restricted to foraging on flowers of Mesembryanthema are dependent upon them. Pollen wasps are expected and dependable visitors in the areas where and at the times when they are nesting. At some such sites and times they are furthermore the most abundant visitors to the stamen carpet and central cone flowers, except for the dark-centered, deep purplish pink species and the crimson-flowered species. Deep purplish pink and crimson "mesem" flowers are most notably visited by monkey beetles (Scarabaeidae: Hopliini), *Peritrichia* species of the *ursus* group (referred to in Gess and Gess 1989 as species of *Anisonyx*, a closely related genus). The cup-shaped flowers of *Herrea* species, which open in the afternoon, although visited by masarines, are more abundantly visited by colletid and halictid bees.

The manner in which the pollen wasps behave on the "mesem" flowers is largely dependent both on the flower type and on the size of the flower in relation to the size of the wasp. Some examples will serve to clarify this point. Although large *Ceramius* species perch on the edge of small cone flowers and insert only the front of the head into the center of the cone, very small pollen wasps such as *Quartinoides* species enter the small cone flowers in the manner suggested by Vogel and Hartmann for large cone flowers. Furthermore, although pollen wasps that are small in relation to

the size of stamen carpet flowers walk around over the anthers and become coated with pollen on the underside, large species of *Ceramius* visiting these flowers "perch" on the side of the flower and only their heads are coated with pollen. Both are equally efficient potential pollinators, as their behavior is constant.

### *Asteraceae*

The Asteraceae is a very large cosmopolitan family containing about one-tenth of the total number of flowering plants (Rendle 1963). The following general account of inflorescence structure and flower structure and behavior is, unless otherwise credited, derived from Rendle (1963).

The flowers of the Asteraceae, generally referred to as florets, are characteristically grouped in heads referred to as capitula. The capitulum is surrounded by few to many involucre bracts. In some species groups of heads are secondarily aggregated into cymose secondary heads (Plate 17). The florets are generally sessile on a common receptacle. All or most of the florets of a head are bisexual or unisexual with the corolla regular, bilabiate, or ligulate. The "daisy" head combines a majority of fertile regular flowers, the disc florets, and an outer "ring" of asexual ligulate florets, giving the capitulum as a whole a flower-like appearance (Plate 16). In some species, groups of capitula are secondarily aggregated into compound cymose heads.

The stamens are generally inserted on the corolla tube. The filaments are generally free and the anthers are united laterally to form a tube and are inwardly dehiscent. The ovary is inferior and the style slender, dividing at the top into two stigmatic lobes bearing hairs on the outer surfaces or at the tip. The style is generally surrounded at its base by a ring-like or shortly tubular nectary. As in the Campanulaceae, the stigmatic lobes are at first closely applied face to face and are surrounded by the anthers. After anthesis the style elongates and the stigmatic head, which is hairy on its outer surface, carries the pollen aloft. Later the stigmatic lobes open, exposing their receptive surfaces. In some species in the absence of insect visitors self-pollination is achieved by the stigmatic lobes curving backward until the receptive surfaces come into contact with the pollen. To a great extent the power of self-pollination has been lost.

Response to tactile stimulation by the anther tube is common. In response the anthers contract and squeeze some pollen out at the upper end.

Small (1915) recorded such sensitivity to touch in 253 of 360 species and varieties examined, among which were represented all the tribes and the majority of the subtribes. In the majority there was, in addition to the presentation of pollen, a lateral movement of the pollen tube toward the touch. Irritability of the style has been recorded for three genera of the tribe Arctotidae of southern Africa (Small 1915). Recovery is rapid and irritability is regained in less than half a minute.

Rendle (1963) gives a good introduction to the biology of the composite capitulum. Marked protandry of the florets, associated with centripetal development in each head, favors crossing between separate inflorescences. In cases where the development of the bisexual florets proceeds slowly from the margin inward, an insect alighting on the head at the margin will, in the early stages of the head, visit pollen-bearing florets only, and, in later stages of the head, will visit florets in the second or female stage before it reaches those in the male stage. Florets, however, open in such quick succession that the head is for a time purely male and for some time purely female. In the comparatively few cases where the florets are unisexual, the outer and first visited are female and the inner functionally male, or the two kinds occur in separate heads.

Vogel (1954) considers that South African composites are generally Hymenoptera-flowers, though flies and certain beetles may also play a large part in pollination. Features which he puts forward to support his Hymenoptera-flower hypothesis are: the presence of nectar which is concealed at a depth of some millimeters only; blue and yellow colors; honey guides in the form of contrasting color between disc and ray florets or contrasting markings at the base of the ligulae; variously produced shine or luster; the possession of honey scent; and the exhibition of "sleeping" movements. He further considers that pollination usually results, on the brush principle, from insects taking up pollen on their ventral surfaces as they crawl around on the capitulum or suck from the disc florets. He furthermore notes that small capitula borne singly on long, flexible stalks are by preference visited by small bees, bombyliids and syrphids. He considers that elongation of the flower tube up to 20 mm and the appearance of scarlet flower color in some Senecioneae and Mutiseae indicate a tendency to psychophily (butterfly pollination).

All six tribes of Asteraceae characteristic of the semi-arid areas of southern Africa are represented in Appendices 1 and 2. The other seven tribes are subtropical, mostly New World or mostly northern hemisphere in



distribution. Generally the flowers are visited by a wide range of insect orders, notably Hymenoptera, Diptera, Lepidoptera, and Coleoptera. The species listed are those whose flowers were found to be visited by Hymenoptera. A wide range of families is represented, among the wasps most notably Braconidae, Chrysididae, Scoliidae, Tiphidae, Pompilidae, Vespidae (Masarinae, Eumeninae, and Polistinae), most families of Sphecoidea, and among the bees Colletidae, Megachilidae, Halictidae, Fideliidae, Anthophoridae, and Apidae.

Only among the pollen wasps and the bees will hymenopterans dependent upon Asteraceae be found. Most of the bee visitors appear to be generalists. A notable exception is the fidelid *Fidelia braunsiana* Friese, which is restricted to the genus *Berkbeya* (Arctoteae) (Whitehead 1984). Among the pollen wasps, 41 percent of which have been recorded visiting Asteraceae, seven species of *Ceramius*, some species of *Jugurtia*, *Quartinia*, *Quartinoides*, and *Quartiniella* are restricted to or show a marked preference for flowers of Asteraceae. Clearly these species are dependent upon the presence of Asteraceae. To what degree their visits are of importance to the flowers that they visit is not clear. Certainly where they occur they are the most dependable visitors and as such can also be depended upon to make successive visits to composite flowers. It has been noted that where a species of masarine is present in large numbers and is actively foraging on a composite, that composite receives few other visitors, although the same species at another site where the pollen wasps are absent may be visited by a wide range of generalist visitors.

Particularly striking in this regard is *Athanasia trifurcata* (Plate 17) (Anthemideae), which grows abundantly in the Clanwilliam district. In the vicinity of nesting areas of *Ceramius braunsi* along the Olifants River to the south of Clanwilliam, it was, in several successive years, almost exclusively visited by this wasp. Similarly, at the same times, in the vicinity of the nesting areas of *Ceramius metanotalis* along the Olifants River to the north of Clanwilliam, it was almost exclusively visited by that wasp. At sites along the Olifants River between the nesting areas of these wasps, *Athanasia trifurcata* was abundantly visited by generalist hymenopterans. It would seem therefore that where they occur in abundance the two *Ceramius* species are important visitors to the flowers of *Athanasia trifurcata* and are undoubtedly efficient pollinators, but that where they do not occur these flowers are undoubtedly efficiently serviced by generalist visitors.



There is no indication that any species of pollen wasps are restricted to a particular genus or species of composite. For example, at some sites in the Clanwilliam district where *Athanasia trifurcata* (Anthemideae) is abundant near the nesting areas of *Ceramius braunsi*, this wasp forages solely on that plant. At other sites where *Arctotis laevis* (Arctoteae) (Plate 16) is also in full flower, it is equally abundantly visited by *Ceramius braunsi*. Preferences are, however, shown. *Pentzia* (Anthemideae) species flowering abundantly in nesting areas are rarely visited. At sites in the Nieuwoudtville district where nesting *Ceramius toriger* and nesting *Quartinia vagepunctata* are abundant, *Pteronia divaricata* (Astereae), *Pentzia suffruticosa* and *Cotula leptalea* (both Anthemideae), *Berkheya fruticosa* (Arctoteae), *Osteospermum oppositifolia* (Calenduleae), *Senecio* prob. *nivea* (Senecioneae), and *Relbania pumila* and *Leysera gnaphalodes* (both Inuleae) flower simultaneously. *Ceramius toriger* forages on the deeper, more robust capitula of the *Pteronia* and *Berkheya* species, whereas *Quartinia vagepunctata* forages on the smaller, shallower capitula of the *Relbania*, *Leysera*, *Senecio*, *Cotula*, and *Pentzia* species.

The behavior of a pollen wasp on a capitulum is governed by the size of the wasp and the diameter of the capitulum. As a general rule, the larger pollen wasps (notably *Ceramius* species) forage by preference on composites with relatively wide, deep capitula, and the smaller pollen wasps (most notably species of the *Quartinia* group) forage on composites with relatively smaller, shallower capitula. As a general rule, the diameter of the capitulum therefore allows the wasp to alight on the upper side of the capitulum and stand on all six legs. While taking nectar it inserts its tongue into one floret after another, the insertion and removal resulting in a bobbing motion. When ingesting pollen it rotates its short, curved front legs in such a way that pollen is brushed toward the mouth. When engaged in both these operations, the wasp is liberally coated with pollen on its undersurface (Fig. 53) and will, when it visits another capitulum, transfer pollen to stigmas presenting their receptive surfaces. The activities of the wasp will furthermore be a sufficient stimulus to trigger the "irritable" behavior of arctotid flowers. When the length of the pollen wasp is considerably in excess of the diameter of the capitulum, the wasp "perches" on its rim. In such instances, for example when *Ceramius* species visit *Pteronia*, only the head, the prosternum, and the bases of the front legs will receive a coating of pollen. Given the regular behavior of the wasps, however, this would be sufficient for transfer of pollen from one

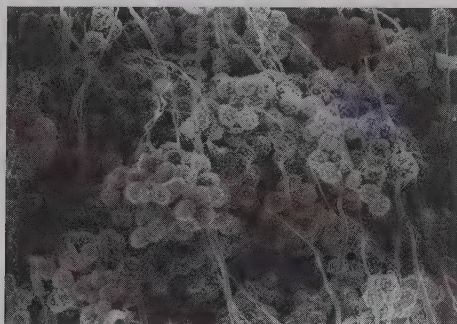
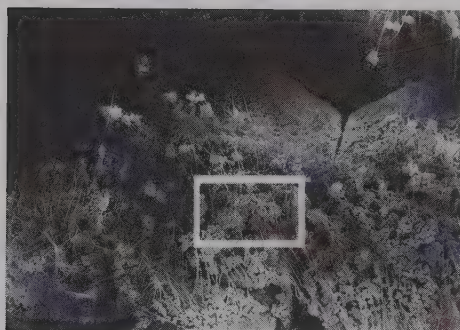


Figure 53. *Ceramius braunsi*: ventral view of anterior half of wasp showing pollen of *Arctotis laevis* (Asteraceae: Arctoteae) on hairy underside ( $\times 8$ ) (top); part of prosternum and base of front legs ( $\times 21$ ) (middle); boxed area  $\times 105$  (bottom).

capitulum to another. Pollen wasps are thus potentially efficient pollinators. As a general rule, the composites have a wider distribution than their pollen wasp visitors but are visited by more than one species of masarine and by different masarines in different areas throughout their range. For example, *Athanasia trifurcata* is visited by *Ceramius braunsi* to the south of Clanwilliam, *Ceramius metanotalis* to the north of Clanwilliam, and by *Ceramius toriger* in the southern Tankwa Karoo to the south of Sutherland. Certainly in areas where pollen wasps specializing in Asteraceae are common, they are probably important potential pollinators of the plants which they visit, indeed in some areas probably the most important potential pollinators.

### *Papilionaceae*

The family Papilionaceae is a very large cosmopolitan assemblage of herbs, shrubs, and trees, most diverse in the warm-temperate regions of the northern and southern hemispheres. It is the youngest of the three families of the Fabales (Cronquist 1981).

The flowers are characteristically "pea flowers," having one free posterior petal, which is the standard or vexillum; two lateral petals, which form the wings or alae; and an anterior pair of petals, which are closely adpressed, often more or less coherent, and which form the keel or carina in which the stamens and the single carpel are enclosed (Cronquist 1981).

The Papilionaceae have been sampled for self-incompatability. An overall high frequency of self-incompatability in woody groups in both the temperate and tropical regions has been identified (Arroyo 1981). In the truly zygomorphic, bilateral papilionoid flower, both pollen and nectar are concealed and become available only after tripping (Arroyo 1981). The tripping requirement has not only led to pollen and nectar economy, but has also precipitated the development of relationships with increasingly specialized pollinators capable of working the successively more complex mechanisms (Arroyo 1981).

It is generally considered that the Papilionaceae are bee-pollinated and that they have been associated with bees throughout their evolutionary history. Arroyo (1981) considers that melittophilous legumes as a whole may be classed as "generalist," in that they are pollinated by a wide range of bees and dependence on a limited number of bees is uncommon. She states further that within the broad category of generalist, relationships

between bees and legumes are diverse and complex, and that potential pollinators of the legume family cut across the entire spectrum of bees. Of particular interest is her statement that comparative data for the South African and Australian regions are few but that nevertheless Scott-Elliot's (1890–1891) notes for Madagascar and South Africa rarely mention more than two or three species of bees on papilionoid legumes. This is clearly at variance with the present findings (Appendix 2), most notably those for *Aspalathus spinescens*, since visits by up to 16 species of bees have been recorded.

### Crotalariaeae: Cape Group

The Crotalariaeae are essentially African, although a few genera extend to the Mediterranean Region, India, Australia, and South America. The greatest generic diversity is centered in southern Africa. Thirteen of the 15 genera are represented in this region (van Wyk 1991). Four genera, *Aspalathus*, *Lebeckia*, *Wiborgia*, and *Rafnia*, constitute the Cape Group of Polhill (1981). This grouping, based on morphological characters, is upheld by the cladistic analysis, using both morphological and chemical characters, of van Wyk and Verdoorn (van Wyk 1991). The analysis further indicates a close subgrouping of *Aspalathus*, *Lebeckia*, and *Wiborgia* separately from *Rafnia*.

Van Wyk (1991) stated that for the Crotalariaeae, despite ongoing taxonomic research, virtually no biological information has been added to the literature.

In the present study, some aspects of which have been published (Gess and Gess 1994), we sampled six species of *Aspalathus*, two species of *Wiborgia*, two species of *Lebeckia*, and one species of *Rafnia* for flower visitors (Appendices 1 and 2). All are shrubs with relatively small, yellow "pea flowers." In some species of *Aspalathus*, notably *Aspalathus spinescens*, and in *Lebeckia sericea*, the petals change to a reddish hue as the flowers age. This color change apparently follows pollination and increases pollination efficiency by discouraging nonproductive visits (Vogel 1954; Arroyo 1981).

### *Aspalathus*

The genus *Aspalathus* is mostly restricted to the Cape fynbos, though a few outliers extend to the Transkei and Natal (van Wyk 1991) (Fig. 20). Of



the species investigated in the present study, five—*A. divaricata*, *A. linearis*, *A. pulicifolia*, *A. spinescens*, and *A. vulnerans*—are endemic to the southwestern Cape (Dahlgren 1988). *A. subtingens* ranges from Laingsburg in the west to the Albany and Somerset East divisions in the east (Dahlgren 1988).

Our observations of flower visitors were made at the height of the flowering season of the *Aspalathus* species, early summer (the last week of September to the second week of October) in the western Cape and late summer (February to March) in the eastern Cape. In addition, visitors to the flowers of *A. spinescens* were sampled in the Clanwilliam district at the start of the flowering season, mid-September. All five western Cape species were visited by pollen wasps and megachilid and/or anthophorid bees, with the exception of *A. vulnerans*, for which observations were probably too limited, only *Masarina familiaris* having been recorded from this species. Additional visitors recorded were eumenines, sphecoids, tiphids, chrysidids, scoliids, and honeybees. *A. subtingens* was observed only at the eastern extension of its range, in the Grahamstown district, where it was visited by megachilid and anthophorid bees. Additional visitors recorded were eumenines, halictids, and honeybees.

The pollen wasps involved in late September and October in the Clanwilliam district were *Ceramius clypeatus*, *Ceramius micheneri*, *Ceramius richardsi*, *Ceramius braunsi*, *Masarina familiaris* and *Masarina mixta*. Of these, *C. clypeatus* and *C. micheneri* seem to be restricted to foraging on *Aspalathus* species, as they have not been found visiting flowers of any other plants even though plants of the other families favored by pollen wasps were flowering abundantly in association with *Aspalathus*. Furthermore, samples of cell provision were found to contain pollen solely matching that of *Aspalathus* species. *Masarina familiaris* is less restricted, having been found in other areas visiting the flowers of *Lebeckia* and *Wiborgia* in addition. It has not, however, been found visiting any flowers other than those of the Cape Group of the Crotalariaeae. Samples of cell provision from sites in the Clanwilliam district contained solely pollen matching that of *Aspalathus*. *Ceramius braunsi* and *Masarina mixta* are casual visitors to *Aspalathus*, the usual forage plants of *C. braunsi* being composites and those of *M. mixta* being *Wahlenbergia* species.

At the start of the flowering season of *A. spinescens* a similar guild of visitors—masarines, megachilids, anthophorids, eumenines, and honeybees—is present. The identity of the masarines, however, differs. The only



species represented is *Masarina hyalinipennis*, an early-flying species, whose flight period is over by the height of the flowering season.

Two behavior patterns are exhibited by pollen wasps when visiting the flowers of *Aspalathus* species, one pattern being consistently followed by the *Ceramius* species and the other by the *Masarina* species.

A *Ceramius*, when alighting on the flower, grasps the alae with the second and third pairs of legs and curves the abdomen down beneath the flower for balance (Fig. 54a, Plate 18). Perched in this way, it inserts its tongue at the base of the standard to reach the nectary. In so doing it trips the flower. The carina opens and the essential parts curve upward to make contact with the bases of the front legs, which are held folded beneath the wasp, and with the prosternum. A considerable amount of pollen is deposited on these hairy surfaces (Fig. 55), and as the wasp consistently positions itself in the same manner it is ideally suited to transfer pollen from the anthers of one flower to the stigma of another. When collecting pollen for provision, it grasps the alae with its second and third pairs of legs and balances itself in much the same manner as it does when alighting on the flower preparatory to imbib-

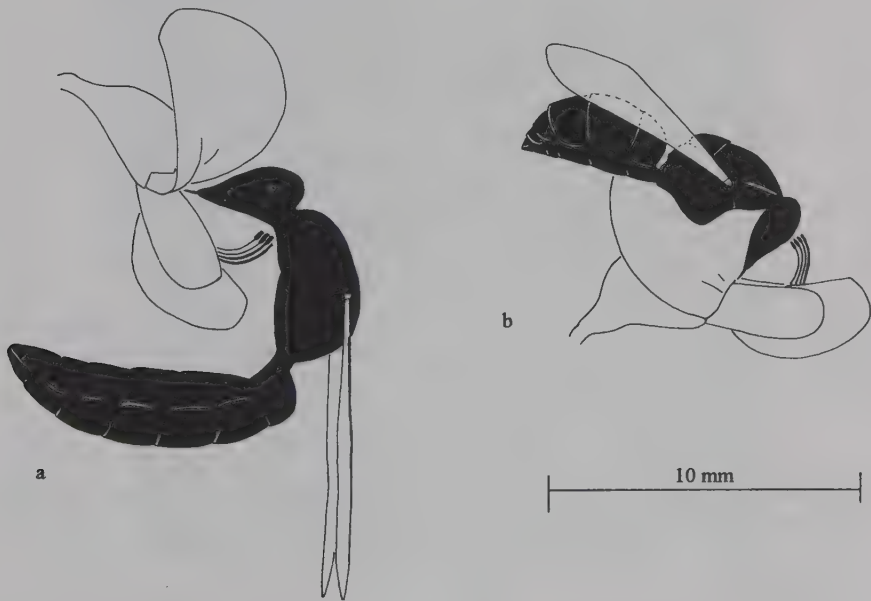


Figure 54. *Ceramius clypeatus* (legs omitted) in nectar-drinking position on flower; (b) *M. familiaris* (legs omitted) in nectar-drinking position on flower.

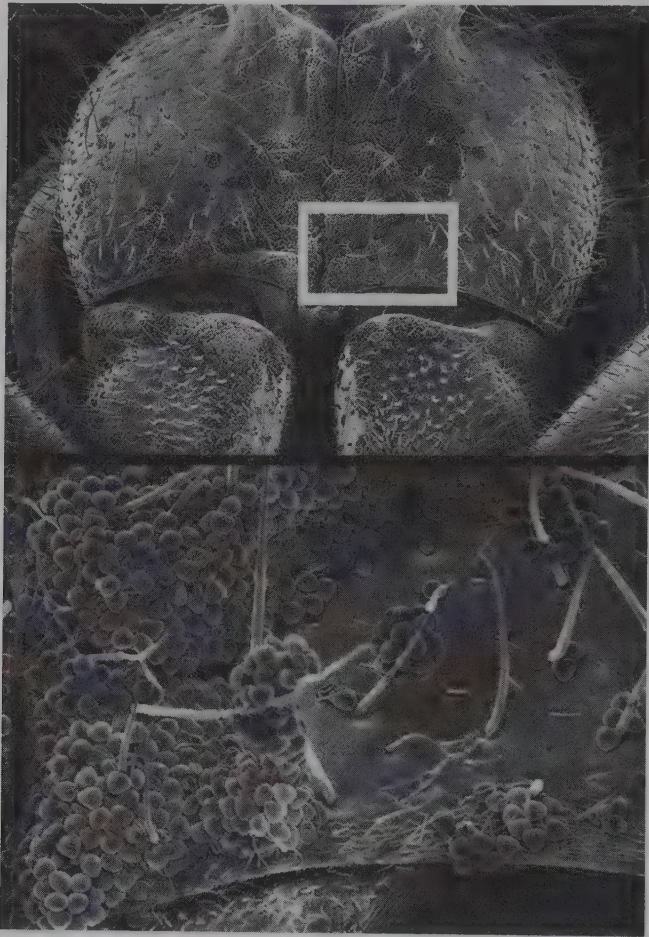


Figure 55. *Ceramius clypeatus*: prosternum and base of front legs (top), showing area of impact with anthers of *Aspalathus spinescens* (Papilionaceae: Crotalarieae) ( $\times 30$ ); boxed area  $\times 150$  (bottom).

ing nectar. It ingests the pollen directly from the anthers. A firm footing on the small, curved alae is aided by the sculpturing of the petal surface, a common feature in Papilionaceae (Stirton 1981).

A *Masarina*, a much smaller visitor than the *Ceramius* species, adopts a completely different stance on the flowers. Instead of alighting on the alae it alights on the standard in such a way that it faces down toward the center

of the flower (Fig. 54 b). When imbibing nectar it inserts its tongue into the flower at the base of the standard to reach the nectary. This causes the carina to open and the essential parts to curve upward to come firmly into contact with the frons of the wasp so that it receives a considerable load of pollen (Fig. 56). As the wasp always positions itself in the same manner, it is ideally suited to transfer pollen from the anthers of one flower to the

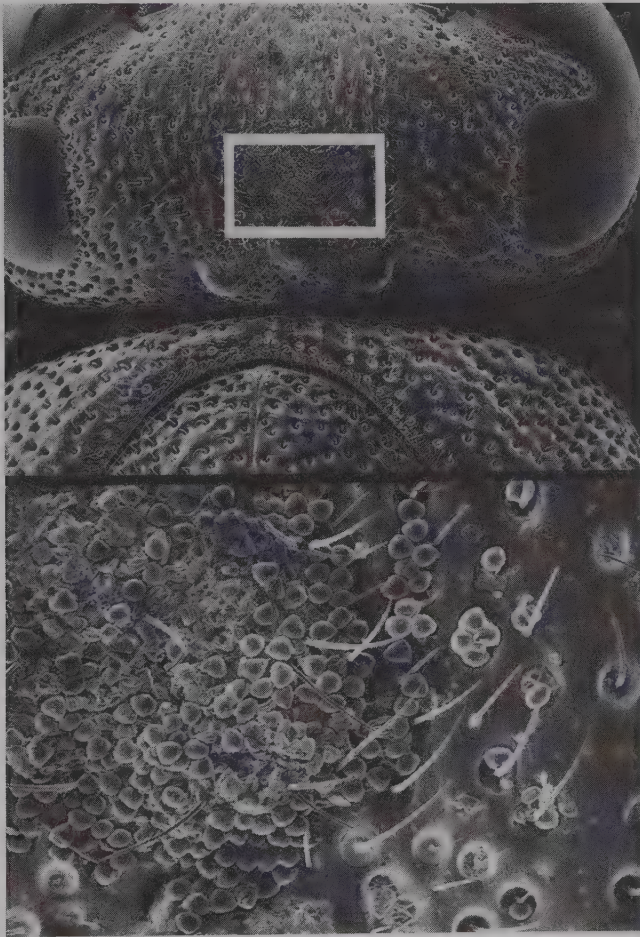


Figure 56. *Masarina familiaris*: dorsal view of posterior portion of head (top), showing area of impact with anthers of *Aspalathus spinescens* (Papilionaceae: Crotalarieae) ( $\times 30$ ); boxed area  $\times 150$  (bottom).



stigma of another. When collecting pollen, the wasp alights on the standard in the same manner and from this position ingests pollen directly from the anthers.

The combination of two methods of triggering the flowers is akin to that recorded by Stirton (1977) for *Canavalia virosa* (Papilionaceae). This species is pollinated by two size categories of bees which, like the *Ceramius* species and the *Masarina* species, have different strategies for operating the flowers.

Where *Ceramius clypeatus*, *Ceramius micheneri*, and *Masarina familiaris* occur, they can be very numerous and the most abundant visitors to *Aspalathus*. This was most certainly the case when observations of visitors to *Aspalathus spinescens* growing on a slope above the Clanwilliam Dam were made during the second week of October 1987 and the first week of October 1988. At those times *C. clypeatus* and *M. familiaris* were the commonest visitors to the flowers of these plants. Furthermore, their daily period of foraging activity was remarkably long, being from 9:30 to 17:30. *C. clypeatus* and *C. micheneri* have very limited distributions (Chapter 2) within the distribution of *Aspalathus* as a genus (Fig. 20). *M. familiaris* occurs throughout a greater part of the range of *Aspalathus*. The presence of *Aspalathus* is probably essential for the successful nesting of *C. clypeatus* and *C. micheneri*, and where these two wasps occur it is likely that they play an important part in the pollination of *Aspalathus*. *M. familiaris* and *M. hyalinipennis* are less dependent on *Aspalathus*, as they will also forage on other papilionates, having been recorded in Namaqualand from *Lebeckia* and *Wiborgia*. However, when foraging on a particular species they are constant visitors, there being little overlap in the areas of occurrence of their various forage plants. In the case of *Aspalathus*, at least, this is explained by the marked individual preferences of *Aspalathus* species for specific soil types (Dahlgren 1988).

The recorded megachilid visitors were *Branthidium braunsi*; *Carinanthidium cariniventris*; six *Chalicodoma* species, *C. aridissima*, *C. fulva*, *C. karoensis*, *C. murina*, *C. schultessi*, and *C. sinuata*; *Immanthidium junodi*; two *Megachile* species, *M. sp. B* and *M. sp. C*; *Oranthidium sp.*; *Serapista rufipes*; and three *Spinanthidium* species, *S. neli*, *S. trachusiforme*, and *S. volkmanni* in the western Cape and *Coelioxys penetratrix*; and three *Megachile* species, *M. gratiosa*, *M. semiflava*, and *M. spinarum*, in the eastern Cape. The recorded anthophorid visitors were *Allodape friesei*; three *Ceratina* species, *C. sp. H*, *C. sp. F*, and *C. sp. J*; and four *Xylocopa* species,

*X. caffra*, *X. capitata*, *X. lugubris*, and *X. rufitarsis* in the western Cape; and *Allodape rufogastra/exoloma*; *Allodapula variegata*; and *Halterapis nigrinervis* in the eastern Cape. All these are generalist flower visitors (S. K. Gess 1992b), which though not dependable visitors are nonetheless expected visitors to papilionate flowers. When visiting *Aspalathus* flowers, they alight in a manner similar to that of the *Ceramius* species and like them trigger the opening of the carina and receive a pollen load on the ventral surface, the positioning of the pollen being dependent on the size of the visitor. If making successive visits, they would successfully transfer pollen from the anthers of one flower to the stigma of another. Many of these bees are more widely distributed than the pollen wasp visitors, and it seems likely that together with the pollen wasps they constitute a guild of potential pollinators of *Aspalathus*.

Honeybees are often prominent among the visitors to *Aspalathus*. Unlike the pollen wasps and the megachilid and anthophorid bees, they do not, however, have a set way of entering the flowers. They rarely trigger the opening of the carina and certainly, if they were to receive a pollen load, would be unlikely to transfer pollen from one flower to the stigma of another. They are therefore nectar thieves.

The remaining wasp visitors are casual and as such are unlikely, except by chance, to effect pollination.

### *Lebeckia*

The genus *Lebeckia* is restricted to Namibia, Botswana, and the Cape Province (van Wyk 1991) (Fig. 20). This genus is considered by Polhill (1976) to be the least specialized in the Crotalariaeae.

Brauns (1926) stated that *Lebeckia* nourishes a great number of bees, the majority of which are of western Cape origin. He further stated that *Chalicodoma murina* and *Chalicodoma karoensis* appear to be bound to *Lebeckia pungens* at Willowmore.

We observed two species of *Lebeckia* for flower visitors: *Lebeckia sericea* in the Springbok District during the first two weeks of September 1992 (at the height of its flowering season) and the second week of October 1989 (toward the end of its flowering season), and in the Kamieskroon district during the second and third weeks of September 1992; and *Lebeckia spinescens* in the Springbok district during the second week of September 1992.



During both September and October there was an overall similarity in the guild of flower visitors to *Lebeckia sericea*: a single species of *Masarina*, several species of megachilids, honeybees, occasional anthophorids and small eumenines. There was, however, species replacement. The *Masarina* in the September samples was, as in the samples from *Aspalathus* to the south, *M. hyalinipennis*, and that in the October samples was *M. familiaris*. The megachilids in the September samples were *Carinanthidium cariniventre*, *Chalicodoma karooensis*, *Chalicodoma murina*, *Spinanthidium bruneipes*, *Spinanthidium trachusiforme*, and *Spinanthidium volkmanni*, whereas those in the October samples were *Chalicodoma bullata*, *Chalicodoma fulva*, *Chalicodoma murina*, *Serapista rufipes*, and *Spinanthidium volkmanni*.

The flowers are much larger than those of the *Aspalathus* species visited. Of particular note is that the carina is much longer. The *Masarina* species alight on the flower in the same manner as they do on *Aspalathus* flowers, but when they insert the tongue at the base of the standard to obtain nectar they do not trigger the opening of the carina. Even if the carina were to open, because of the relative sizes of wasp and flower, the wasp would not receive a load of pollen. Clearly, whereas in their nectar-collecting visits to *Aspalathus* the *Masarina* species are potential pollinators, in their visits to *Lebeckia sericea* they are thieves. It is, however, of note that, when collecting pollen, the *Masarina* species walk outward along the keel and in so doing trip the flower. The megachilids, as when visiting *Aspalathus*, alight on the alae and insert their tongues at the base of the standard when collecting nectar. In so doing they cause the carina to open and they receive a load of pollen on the ventral surface. As they always alight in the same way, they have the potential to pollinate the flowers by transferring pollen from one flower to the stigma of another. As already noted, they are generalists and therefore not necessarily dependable visitors, although they are clearly expected visitors.

Honeybees visiting *Lebeckia sericea* seem to be less able than they are on *Aspalathus* flowers to obtain nectar without positioning themselves in such a manner that they trip the flowers. They should therefore be considered to be among the potential pollinators, particularly where there are large patches of *L. sericea*, reducing the likelihood of lack of constancy.

The eumenines, though a regular constituent of the guild of visitors, are too small to trigger the flowers.

The flowers of *Lebeckia spinescens* are of comparable size to those of the *Aspalathus* species. They, too, were being visited in the main by *Masarina*

*hyalinipennis* and megachilid bees, *Chalicodoma karooensis*, *Spinanthidium volkmanni*, *Spinanthidium trachusiforme*, and *Spinanthidium neli* having been represented in the samples. The flowers are small and so are tripped by *M. hyalinipennis*, which therefore should, with the megachilid bees, be considered to be a potential pollinator. *L. sericea* and *L. spinescens* are unlikely to compete for visitors, as the former grows on stony slopes and the latter in level, sandy situations.

### *Wiborgia*

The genus *Wiborgia* is restricted to the western and southwestern Cape Province (van Wyk 1991) (Fig. 20). It is almost indistinguishable from some of the woody species of *Lebeckia* except for the winged, samara-like fruit (van Wyk 1991).

We recorded flower visitors from *Wiborgia monoptera* in Namaqualand, in the Kamieskroon district in mid-September 1992 and the Springbok district during the second week of October 1989, and from an unidentified *Wiborgia* species at the southern end of the Tankwa Karoo, 43 km ENE of Ceres during the first week of December 1989. The flower-visiting guilds were constituted similarly to those visiting *Aspalathus* and *Lebeckia*. They included most notably a masarine, megachilids, and eumenines from *W. monoptera* and megachilids, anthophorids, a colletid, and eumenines from *W. sp.* (Appendix 2).

In September the pollen wasp was again *Masarina hyalinipennis* and the megachilids were *Chalicodoma karooensis* and *Chalicodoma murina*. In October the pollen wasp was again *Masarina familiaris* and the megachilids were *Chalicodoma fulva*, *Spinanthidium trachusiforme*, and *Spinanthidium volkmanni*.

The flowers are small, of comparable size with those of *Aspalathus* and *Lebeckia spinescens*, and therefore the two pollen wasps can similarly be included with the megachilids as potential pollinators.

### *Rafnia*

The genus *Rafnia* is found from the southwestern Cape through to Natal (van Wyk 1991) (Fig. 20).

*Rafnia amplexicaulus* is a frequent constituent of dry fynbos in the Clanwilliam district. We observed it for flower visitors in two areas in this

district during the last week of September 1985, the first week of October 1990, and the second week of October 1987. A very limited range of insects was recorded: no masarines; two large anthophorids, *Xylocopa capitata* and *Xylocopa caffra*; one large megachilid, *Chalicodoma cincta*; and a eumenine, *Synagris maxillosa bequaerti*. All were regular visitors and the bees were most certainly potential pollinators.

## Evaluation

From a consideration of the guilds of visitors to the flowers of the four genera of the Cape Group of the Crotalariaeae, certain similarities are immediately apparent. All are visited by megachilids, principally species of *Chalicodoma* and *Spinanthidium*, which for all genera are expected visitors and potential pollinators. Anthophorids are less common visitors except to *Rafnia amplexicaulis*, to which two large carpenter bees, *Xylocopa capitata* and *Xylocopa caffra*, are expected visitors and potential pollinators.

*Masarina familiaris* and *Masarina hyalinipennis* within their distribution ranges are dependable visitors to *Aspalathus*, *Lebeckia*, and *Wiborgia* and are potential pollinators of the smaller-flowered species. *Ceramius clypeatus* and *Ceramius micheneri* within their limited distribution ranges are dependable potential pollinators of flowers of *Aspalathus*, at least of *A. spinescens* and *A. pulicifolia*.

Honeybees and eumenines are expected visitors but are probably of little importance as pollinators.

## Campanulaceae

The family Campanulaceae is mainly temperate and subtropical in distribution. There are two well-marked subfamilies, the Campanuloideae and the Lobelioideae, connected by a small group of transitional genera that are sometimes treated as a third subfamily, Cyphioideae (Cronquist 1988). The flowers of the Campanuloideae are regular and the anthers are generally free. The Lobelioideae are the more advanced group, marked by their highly irregular, resupinate flowers and connate anthers (Cronquist 1988). Of the southern African pollen wasps, 18 percent have been recorded as visitors to flowers of Campanulaceae of the subfamilies Campanuloideae and Lobelioideae. All but one, a species of *Celonites*, which

seems to be associated with *Lobelia arenaria* (Lobelioideae), are associated with the genera *Wahlenbergia* and *Microcodon* (Campanuloideae).

*Wahlenbergia*, with which at least 16 species of southern African masarines are associated, is in the main African. About 200 species are known and of these nearly 150 occur in southern Africa, the greatest concentration of species being in the southwest. *Microcodon*, a genus closely related to and easily confused with *Wahlenbergia*, is known from four species, all endemic to the southwestern Cape. The following general account of *Wahlenbergia* flower structure and "behavior" is derived from Thulin (1975) except where otherwise credited.

*Wahlenbergia* plants are mostly annual or perennial herbs, the majority of which are erect though some are straggling. Some have woody bases. The number of calyx lobes, corolla lobes, and stamens is almost invariably five. The corolla is in many species campanulate with a distinct corolla tube and more or less broad lobes. From this probably generally primitive state, there is a tendency toward a shortening of the tube to an almost choripetalous state and the narrowing of the lobes to give the corolla a stellate appearance. The stamens alternate with the petals. In some species filament bases are expanded. The anthers are either free or attached to the corolla. The position of the ovary varies from inferior to subsuperior. Thulin notes considerable intraspecific variation. The lower part of the style is glabrous or hairy with normal hairs, and the upper part is variously clad with pollen-supporting hairs, as in other members of the family.

Protandry is a pervading characteristic of *Wahlenbergia*, as well as of other members of the Campanulaceae. In the bud the ripe anthers form a tube through which the style grows, pushing the stiff pollen-collecting hairs through the thecae and clearing them of the pollen, which adheres to the style in the open flower. Nectar is produced on the top of the ovary.

The mechanism of pollen presentation strongly favors cross-pollination and allogamy. According to Thulin, self-incompatibility was proved in progeny of *W. androsacea* (which he considers probably to be conspecific with *W. annularis*) from Namaqualand and Namibia. In these plants seed-setting occurred only after artificial cross-pollination. In other taxa tested, namely *W. abyssinica* (tropical Africa southward to Natal), *W. hirsuta* (tropical Africa, India, and Nepal), *W. krebsii* subsp. *arguta* (west Africa), *W. lobelioides* subsp. *lobelioides* (Madeira, Canary Islands, Cape Verde Islands), *W. pusilla* (higher mountains of Ethiopia, Kenya, and Tanzania), and *W. silenoides* (uplands of tropical Africa), all outside the area presently



under consideration, self-pollination and subsequent autogamy generally occurred by the recurving of the style lobes, which enabled the stigmatic surface to come into contact with the pollen of the same flower.

Little has previously been noted concerning visitors to the flowers of *Wahlenbergia*. Michener (1965) recorded colletid and halictid bees visiting *Wahlenbergia* in Australia. The bees' association with the flowers was apparently oligolectic. Unfortunately, the species of *Wahlenbergia* was not recorded. Thulin (1975) stated that no information about insects visiting flowers of *Wahlenbergia* in Africa seemed to exist except for a note, "worked by bees for nectar," on the collection of Friend 361 of *W. napiformis* (a species with a short tube and broadly expanded filament bases).

Vogel (1954) noted that he often observed Hymenoptera the size of honeybees engaged in the pollination of *Wahlenbergia* species in the Cape. He also stated that it is possible that in the genus *Wahlenbergia* fly-loving (myiophilous) forms may occur.

Struck (1990 and 1994) listed insect visitors to two species of *Wahlenbergia* but recorded no observations concerning the comparative structure of the flowers or the behavior of the insects at the flowers. He did, however, indicate whether one or more individuals was involved and in some instances gave the results of his examination of the pollen carried by the insects. This latter was recorded as percentage of *Wahlenbergia* pollen and number of types of pollen, which gives one some indication of the constancy of visiting. From a consideration of his tables it is apparent that all species of Hymenoptera examined, other than the honeybees and his *Capicola* sp. 4 (Melittidae), had clearly been visiting a mixture of plants. Honeybees are of course known to be generalists but to show temporary constancy of visiting, if a good resource is located. *Capicola* sp. 4 showed constancy but the sample was too small for any inferences to be made.

In the present study flower visitors to eight species of *Wahlenbergia* and one species of *Microcodon* in the southwestern Cape and one species of *Wahlenbergia* in the eastern Cape were observed and voucher specimens were collected (Appendices 1 and 2).

Two basic flower types were represented, deeply campanulate (Figs. 57a, b, d-h) (*W. psammophila*, *W. ecklonii*, *W. cf. constricta*, *W. paniculata*, *W. pilosa* (Plate 19), *W. prostrata* (Plate 20), *W. sp. N*, and *M. sparsiflorum*) and shallowly campanulate (Figs. 57i-l) (*W. annularis* (Plate 21)). In all species, in the bud and the newly opened flower the receptive surfaces of the stigmatic lobes are closely adpressed. The upper part of the style and the outer surface



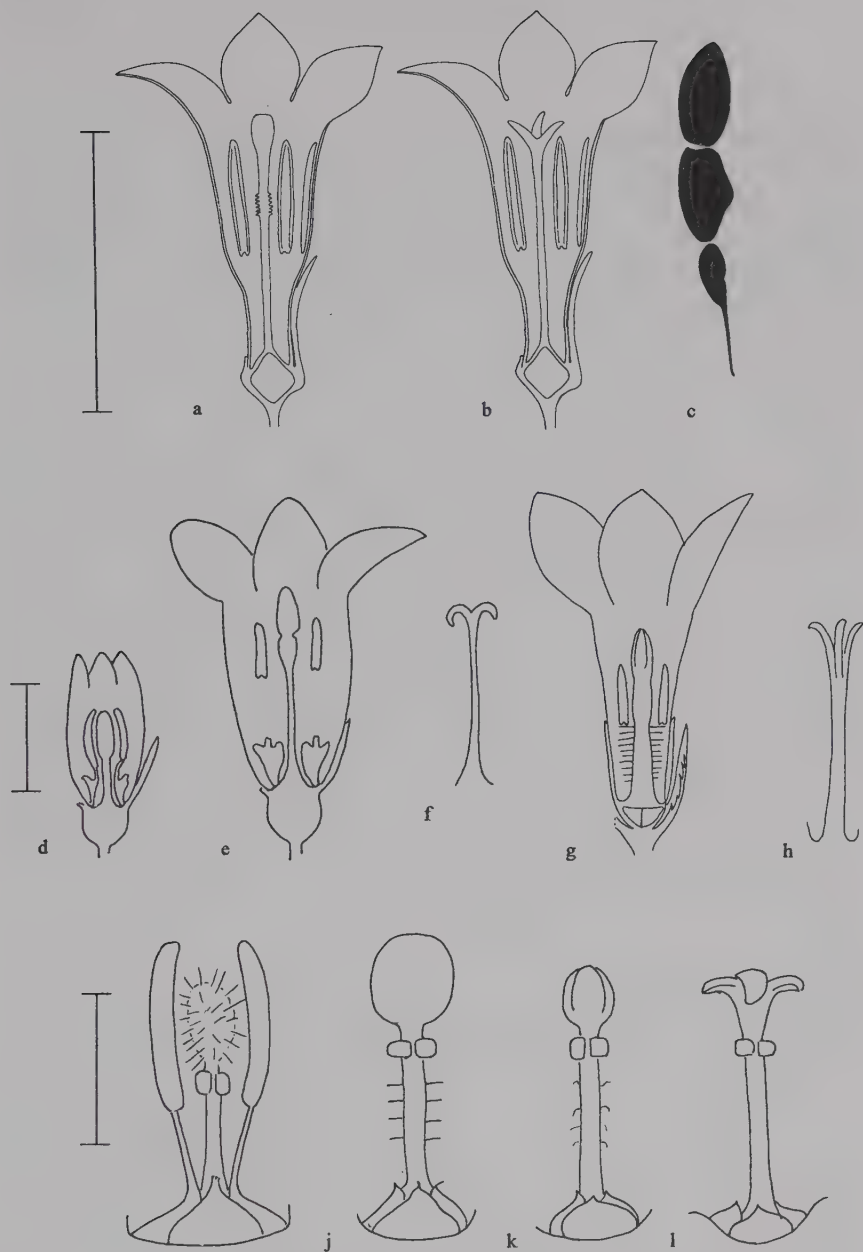


Figure 57. Longitudinal sections of flowers of (a–b) *Wahlenbergia paniculata*; (d–f) *W. psammophila*; (g–h) *W. pilosa*; (i–l) *W. annularis*. (c) *Quartinia parcepunctata*. (Scale bar = 5 mm.)

of the closed stigmatic lobes bear variously arranged, pollen-supporting hairs. The anthers closely surround the style. They dehisce introrsely before the bud opens. In a newly opened flower the pollen coats the upper part of the style and the outer surfaces of the closed stigmatic lobes, giving the whole a club-like appearance. After the flower has been open some little while, the hairs supporting the pollen disappear—apparently by invagination (Cronquist 1981)—and the pollen falls, being retained within the corolla in the deep-flowered species but falling free in *W. annularis*. The style lobes then separate and present their receptive surfaces.

The nectar-secreting tissue on the upper surface of the ovary of all the species with deeply campanulate flowers is uncovered. That of the shallowly campanulate *W. annularis* is covered by the bases of the filaments, which are expanded and closely adpressed to it.

The free lobes of the corolla of the open flowers of all species exhibit “sleeping” movements. The flowers open in mid-morning, close in middle to late afternoon, and reopen toward mid-morning. Wasps and bees making use of this phenomenon for night sheltering were noted.

The importance of the flowers to the pollen wasps and the relative potential of the pollen wasps and the other insect visitors as pollinators of the flowers is considered. To be a potential pollinator an insect must, when visiting a newly opened flower, brush against the pollen-clad style to collect a coating of pollen and then, when coming from such a flower to one in which the stigmatic lobes have spread out, transfer pollen to the stigma.

### *Wahlenbergia paniculata*

*Wahlenbergia paniculata* is a much-branched, low-growing, upright slender annual. At Clanwilliam it grows in extensive patches, being the dominant plant cover in dry fynbos on slopes above the dam in early summer. During the period of investigation, the first to the third weeks of October, it was in full flower together with *Aspalathus spinescens* (Papilionaceae), *Arctotis laevis* (Asteraceae), *Athanasia trifurcata* (Asteraceae), *Pentzia* sp. (Asteraceae), *Coelanthum* sp. (Aizoaceae), *Psilocaulon acutisepalum* (Aizoaceae), and *Crassula dichotoma* (Crassulaceae).

The flowers of *W. paniculata* (Figs. 57a, b) are erect. The corolla, which is violet in color, is deeply campanulate. In the bud and the newly opened flower, the receptive surfaces of the closely adpressed stigmatic lobes form a knob-like tip to the style. The upper two-fifths of the style are hairy,

particularly at the lower end where the hairs are short and robust and form a distinct collar.

Seven species of masarine wasps, *Ceramius socius*, *Masarina mixta*, *Celonites wahlenbergiae*, *Quartinia parcepunctata*, *Quartinia persephone*, *Quartinoides* sp. N, and *Quartinoides* sp. S, one species of megachilid bee, *Hoplitis* sp. C, and five species of bombyliid flies were recorded visiting the flowers (Appendix 2).

*Celonites wahlenbergiae* seems to be closely associated with *Wahlenbergia*, having been found only at sites where *Wahlenbergia* was in flower and to be most notably visiting these flowers. At the Clanwilliam site it was, however, also visiting *Coelanthum* sp. and *Crassula dichotoma*, and in addition has been recorded from *Herrea* sp., *Polycarena* sp., and *Pelargonium* to the west of Clanwilliam. Pollen from the provision from the nest of this wasp investigated at the Clanwilliam site was principally derived from the flowers of *Wahlenbergia paniculata*.

*Masarina mixta* has been recorded principally from *Wahlenbergia*, there being otherwise only a single record from *Aspalathus spinescens* and a single record from *Athanasia trifurcata*. It therefore seems to have a close association with *Wahlenbergia*.

*Quartinia parcepunctata* was an abundant visitor to *W. paniculata* and was not recorded from any of the other flowers. The only other flower-visiting records for this species are from *Wahlenbergia* on the Theronberg Pass, Ceres, and from *Microcodon* to the east of Clanwilliam. It therefore seems likely that it has a close association with *Wahlenbergia* and *Microcodon*.

*Quartinia persephone*, though recorded not only from *W. paniculata* at the Clanwilliam Dam but also from *M. sparsiflorum*, was a less frequent visitor and was in addition, albeit in smaller numbers, recorded from *Psilocaulon acutisepalum* and *Athanasia trifurcata* and, in the Nieuwoudtville district, from *Senecio*. It would therefore appear to be an expected visitor but not a dependable visitor to *Wahlenbergia*.

*Quartinoides* sp. N, though an infrequent visitor to *W. paniculata* during the sampling period, was an abundant visitor to *W.* sp. in the Nieuwoudtville district and has not been recorded from any other flowers.

The record of *Quartinoides* sp. S is for a single male, and as there are no other flower-visiting records for this species no comment can be made.

*Ceramius socius* was represented solely by a single male. It has otherwise been recorded abundantly from *Mesembryanthema*, from which it has been shown to obtain its provision. It is clearly a casual visitor.

Few flower-visiting records are available for *Hoplitis* sp. C. It was an infrequent visitor to *W. paniculata* and there are only single records of visits to *W. annularis* and *Aspalathus spinescens* in the Clanwilliam district and to *W. pilosa* in the Springbok district.

Pollen wasps when visiting the flowers alight on the outwardly curved corolla lobes before entering, so that when they enter a newly opened flower their dorsal surfaces brush against the pollen-clad style and collect a coating of pollen. When a pollen wasp comes from such a newly opened flower and then enters a flower in which the stigmatic lobes have spread out, pollen will be transferred from it to the stigma, making it a potential pollinator.

The pollen wasps collectively seem to represent the most dependable potential pollinators of *W. paniculata*. All would, furthermore, owing to the manner and constancy of their behavior when visiting the flowers, be capable of pollinating them. Given the manner of pollen presentation, the most efficient pollinators will be the species with the best flower fit—that is, those which are of a size small enough to enter the corolla tube but large enough that in doing so they cannot pass the pollen column without pressing against it. The species with the best flower fit will vary with variations in flower size, which in turn varies with availability of water. At Clanwilliam Dam at the time of the study, *Quartinia parcepunctata* had the best flower fit.

The bombyliids hovered above the flowers, imbibing nectar from them through their long proboscises. As they did not enter the flowers, it is unlikely that they received a pollen load and they are therefore not considered here as potential pollinators.

### *Wahlenbergia psammophila*

*Wahlenbergia psammophila* is a relatively sparsely branched upright annual which, as its name indicates, grows in sandy soil. It was observed for insect visitors 11 km to the west of Clanwilliam on the road to Graafwater in an area of dry fynbos with a sandveld element. At this site it was the dominant *Wahlenbergia* species of relatively undisturbed ground. Less common was *W. paniculata*, the dominant species at the Clanwilliam Dam. Where the ground had been disturbed by cultivation, these two species had been replaced by *Wahlenbergia annularis*. During the periods of the investigation, the first two weeks of October, all three *Wahlenbergia* species were in full flower together with *Aspalathus spinescens* (Papilionaceae), *Coelan-*

*thum grandiflorum* (Aizoaceae), *Leucodendron* sp. (Proteaceae), *Herrea* sp. (Aizoaceae), *Helichrysum* sp. (Asteraceae), *Senecio* sp. (Asteraceae), *Polycarena* sp. (Scrophulariaceae), *Pelargonium* sp. (Geraniaceae), and *Monopsis debilis* (Campanulaceae).

The flowers of *W. psammophila* (Fig. 57 e) are larger than those of *W. paniculata*, from which they are also immediately distinct being purplish violet rather than bluish violet. The style bears a marked collar of pollen-supporting hairs and the bases of the filaments, which are free from the corolla, are expanded and hairy. As the flower elongates the anthers, which remain attached to the corolla, tear free from the filaments. The filament bases persist and the nectar is cupped within them.

During the periods of observation the flowers of *W. psammophila* were visited almost solely by pollen wasps. The only other visitor was a single male *Capicola* sp. C (Melittidae), which was observed examining a flower. This bee, being short-tongued and too large to enter the corolla tube, would in any case not be able to reach the nectar and the record was therefore of a "nonvisit."

Three *Celonites* species, *C. latitarsis*, *C. wahlenbergiae*, and *C. bergenwahliae*, were regular visitors from the opening of the flowers in mid-morning to their closing in mid- to late afternoon. Male *Masarina mixta* entered the flowers in late afternoon to sleep and were enclosed within them when they closed for the night.

Although *C. wahlenbergiae* and *C. bergenwahliae* were constantly in attendance at *W. psammophila* flowers throughout the day, they were particularly busy in these flowers in the morning. When afternoon came they also visited, but far less frequently, flowers of *Pelargonium* sp., *Helichrysum* sp. (only *C. wahlenbergiae*), *Senecio* sp. (only *C. bergenwahliae*), *Polycarena* sp., *Coelanthum grandiflorum*, and *Herrea* sp. It should be noted that the flowers of the two species of Aizoaceae only open when the afternoon is well advanced. It is likely that the *Wahlenbergia* flowers have been adequately serviced by the time these wasps become less constant in their visits and that the change in behavior coincides with a falloff in available rewards of pollen and nectar.

*Celonites latitarsis* showed greater flower constancy; apart from one visit to *C. grandiflorum* by a male, it was not recorded visiting any flowers other than those of *W. psammophila*. A nest of this wasp was investigated at this site and the pollen was found to be all of one type and to match that of *W. psammophila*.



The behavior of the *Celonites* species, when visiting the flowers, is the same as that described for pollen wasps visiting the flowers of *W. paniculata*. The *Celonites* are furthermore particularly well suited to effect pollination, as they are small enough to enter the flowers but large enough to fit snugly.

### *Wahlenbergia pilosa*

*Wahlenbergia pilosa* is a much-branched, low-growing annual. Investigation of flower visitors was undertaken at two sites in the Springbok district, one in the Goegab Nature Reserve to the northeast of Springbok and the other at Klipfontein to the southwest in areas of Namaqualand Broken Veld. At these sites *W. pilosa* forms dense patches in clearings between bushes, and in two successive years it was in full flower during the second week of October. Also in flower at both sites was *W. annularis* and various "mesems" (Aizoaceae) and "composites" (Asteraceae), and in the Goegab Nature Reserve *Peliostomum virgatum*, *Aptosimum spinescens*, *Aptosimum lineare* (all three Scrophulariaceae), *Hermannia* spp. (Sterculiaceae), *Lebeckia sericea* (Papilionaceae), and *Monopsis debilis* (Campanulaceae).

The flowers of *W. pilosa* (Figs 57 g, Plate 19) are erect. Their size seems to be dependent on the availability of water when the plants are growing. The corolla, which is deeply campanulate, is "two-tone" bluish violet. The style bears no distinct collar of hairs; however, the upper part of the style and the nonreceptive outer surfaces of the closed stigmatic lobes in the bud and newly opened flower are densely and uniformly covered with stiff pollen-supporting hairs. Thus a relatively long pollen column is presented. The lower part of the style is clothed in persistent long, soft hairs, which extend almost to the corolla and through which a nectar gatherer must reach.

The flowers were visited abundantly by pollen wasps: *Quartinia* sp. E and to a lesser extent *Quartinia* sp. G, *Jugurtia braunsi*, and *Quartinioides* sp. M in the Goegab Nature Reserve; and *Quartinioides* sp. M and to a lesser extent *Jugurtia braunsi* at Klipfontein. In addition to the pollen wasp visits, casual visits by butterflies, a sphecid wasp, *Ammophila punctaticeps*, and a megachilid bee, *Hoplitis* sp. C, were recorded.

The *Quartinia* species and *Quartinioides* sp. M (Plate 20) were recorded from *Wahlenbergia* species only. The *Quartinia* species are known only

from the Springbok district whereas *Quartinoides* sp. M was also recorded as an abundant visitor to *W. prostrata* at Anenous.

*Jugurtia braunsi* is not restricted to *Wahlenbergia*, having also been recorded from Aizoaceae and Asteraceae at both sites in the Springbok district and at sites in the Nieuwoudtville district.

The behavior of the pollen wasps when visiting the flowers is the same as that described for pollen wasps visiting the flowers of *W. paniculata*. The species with the best flower fit varies with variations in flower size, resulting from variations in availability of water during the growing period.

### *Wahlenbergia prostrata*

*Wahlenbergia prostrata* is a low-growing annual herb. At Anenous, to the northwest of Springbok, it grows in patches in clearings between bushes. During the periods of investigation, the second week in October in two successive years, it was in full flower growing together with *Zygophyllum* sp. (Zygophyllaceae), *Peliostomum virgatum* (Scrophulariaceae), *Drosanthemum* sp. (Aizoaceae), *Galenia* sp. (Aizoaceae), and *Leysera gnaphalodes* (Asteraceae).

The flowers of *W. prostrata* are erect. The corolla, which is pale violet in color, is deeply campanulate. The nectary is not covered but to reach it the visitor must push its way between upwardly directed stiff hairs.

A masarine, *Quartinoides* sp. M (Plate 20), a melittid bee, *Capicola* sp. E, and a crabronid, *Belomicroides* sp., were recorded visiting the flowers. All three insects are similarly sized and all gave a good flower fit. One visit by an allodapine bee was recorded, but this bee is too large to enter the flowers.

*Quartinoides* sp. M was the most common visitor. It has also been recorded visiting *W. pilosa* at two sites in the Springbok district. Its behavior, when visiting the flowers, is the same as that described for pollen wasps visiting flowers of *W. paniculata*.

### *Wahlenbergia cf. constricta*

*Wahlenbergia cf. constricta* is an upright, sparsely branched perennial. It was investigated for flower visitors during the first week of October at Klein Alexandershoek near Clanwilliam. At this site it was in full flower growing in clearings in dry mountain fynbos. Also in full flower was *Aspalathus spinescens* (Papilionaceae).

The flowers of *W. cf. constricta* are held erect. The corolla, which is bluish violet in color, is deeply campanulate. The nectary is not covered.

The flowers were being regularly visited by *Celonites bergenwahliae* and to a lesser extent by *Quartinia parcepunctata*, the most abundant visitor to *W. paniculata* at the Clanwilliam Dam. Neither of these pollen wasps was visiting *A. spinescens*, although the flowers of this plant were being visited by *Ceramius chypeatus* and *Masarina familiaris*.

The behavior of the pollen wasps, when visiting the flowers, is the same as that described for pollen wasps visiting the flowers of *W. paniculata*.

### *Wahlenbergia ecklonii*

*Wahlenbergia ecklonii* is an erect or stagging perennial herb. Flowers of this plant were observed for insect visitors during the last week of November at two localities, the Theronsberg Pass and the Gydo Pass, both in the Ceres district. At these localities it was in full flower, as too were *Athanasia trifurcata* and *Berkheya carlinifolia* (both Asteraceae). On the Gydo Pass it was growing among *Aspalathus divaricata* (Papilionaceae), which was also in full flower.

The flowers of *W. ecklonii* are erect. The corolla is deeply campanulate and bluish violet. There is no distinct collar of pollen-supporting hairs. Instead the whole of the upper half of the style and the outer nonreceptive surfaces of the closed stigmatic lobes are covered with stiff, pollen-supporting hairs. Thus a relatively long pollen column is presented. The nectar-secreting tissue is not covered. Nectar is produced extremely abundantly and at the height of production more than half fills the corolla tube so that it is visible as a shining surface from above.

During the periods of observation the flowers of *W. ecklonii* were being visited regularly and most abundantly by pollen wasps, *Celonites capensis* on the Gydo Pass and *Quartinia parcepunctata*, *Quartinia* sp. H, and *Quartinoides* sp. U on the Theronsberg Pass. Also visiting the flowers on the Theronsberg Pass but in smaller numbers were two halictids, *Lasioglossum* sp. H and *Nomioides ?maculiventris*, an ant, *Camponotus* sp., a syrphid fly, a small ?lygaeid bug, and three small beetles, including a chrysomelid and a malachid.

*Celonites capensis* and *Nomioides ?maculiventris* are known to visit, in addition, flowers of families other than Campanulaceae. *C. capensis* has been collected from flowers of *Phyllopodium cuneifolium* (Scrophulariaceae),

*Ebretia rigida* (Boraginaceae), and *Berkheya* (Asteraceae) in the Grahamstown district and of *Pelargonium myrrhifolium* (Geraniaceae) and *Berkheya* (Asteraceae) in the Oudtshoorn district. *N. ?maculiventris* has been collected from the flowers of *Athanasia* (Asteraceae) and *Euclea* (Ebenaceae) 43 km ENE of Ceres. *Quartinia parcepunctata*, on the other hand, has only otherwise been recorded from the flowers of Campanuloideae: *W. paniculata*, *W. cf. constricta*, and *M. sparsiflorum*.

When the flowers are well charged with nectar, the visitors cannot enter but alight on the lip of the corolla and from this position imbibe nectar. The pollen wasps were noted also to be collecting pollen while standing thus. Such an overabundant nectar production seems to be disadvantageous to a plant attracting insects for the purpose of pollen transfer.

### *Wahlenbergia annularis*

*Wahlenbergia annularis* is an annual herb. It has a basal rosette of leaves and tall, upright, sparsely branched inflorescence stems. In the Springbok, Clanwilliam, and Citrusdal districts it grows sparsely in undisturbed areas but abundantly in disturbed ground, where it is often the dominant pioneer plant.

The flowers are held upright and singly. The corolla, which is shallow and widely campanulate, is pale violet generally with a pronounced darker violet streak on the lower half of each of the corolla lobes. In the bud and the newly opened flower the closed stigmatic lobes, which are markedly hairy on their outer, nonreceptive surfaces, form a knob-like tip to the style. Below the knob the style is encircled by three "cushions" (glands according to Thulin 1975). Beneath the ring of glands the style is slender and clad in short, sparse hairs. In the bud the anthers, which are free from the corolla, are held upright and closely surround the style and closed stigmatic lobes (Fig. 57 i). The bases of the filaments are broadly expanded and adpressed to the upper, nectar-producing surface of the ovary, which they completely cover. The anthers dehisce within the bud. The pollen coats the upper portion of the style and the nonreceptive outer surfaces of the closed stigmatic lobes, giving it a club-like appearance. After the flower has been open some while the hairs supporting the pollen disappear and the pollen falls away. The anthers shrivel and fall away, leaving, however, the expanded filament bases covering the nectar. Still later the stigmatic lobes open and curve back, exposing their receptive surfaces.



The flowers were most frequently visited by two large melittid bees, *Capicola* sp. A and *Capicola* sp. C (Plate 21), which enter the flowers directly, orientated such that the ventral surface is toward the style. They are thus able to penetrate under the filament bases covering the nectary and are also suitably positioned for collecting pollen. They are ideally suited to pollinating the flowers. When collecting nectar from a freshly opened flower, the bee receives a pollen coating on the ventral surface. When it later enters a flower in which the stigmatic lobes have opened, pollen will be transferred from the bee to the receptive surfaces.

Pollen wasps were noticeably absent apart from a single instance of a visit by *Masarina mixta*. It seems probable that the nectar and pollen of these flowers, unlike those of the deeply campanulate flowers, is not available to pollen wasps. As they alight on a corolla lobe and then enter with the dorsal surface toward the style, the nectar would be almost entirely closed to them. Furthermore, the pollen before it falls would be beyond reach, and afterward it would be unavailable as it falls free.

#### *Wahlenbergia* sp. N

*Wahlenbergia* sp. N could not be identified to species by Jo Beyers, who, however, noted on the determination label that "ovary 5 locular, opposite the calyx lobe therefore *Wahlenbergia*. (looks very much like *Microcodon glomeratum* !)." It is a low-growing, much-branched perennial herb. It was investigated for flower visitors during the last week of September in an area of fynbos at a site between Nieuwoudtville and the escarpment to the west. At the time of sampling the plants were flowering abundantly in clearings between bushes together with *Homeria* sp. (Iridaceae) and *Wachendorfia* sp. (Haemodoraceae) and an occasional plant of *Lobelia linearis* (Campanulaceae). The notable flowering shrubs at the site were *Paranomus bracteolaris* (Proteaceae) and *Aspalathus linearis* (Papilionaceae).

The flowers of *Wahlenbergia* sp. N are smaller than those of the other species and are presented in clusters. The corolla, which is deeply campanulate, is pale violet. The style bears no distinct collar of pollen-supporting hairs. Nectar is very abundantly produced and the nectar secreting tissue is not covered.

On September 29, 1990, *Quartinoides* sp. N, which was also recorded visiting *Wahlenbergia* in the Clanwilliam district, appeared to be the sole visitor to the flowers and was visiting them and solely them in large



numbers. On the next day *Podalonia canescens* (Sphecidae), a generalist flower visitor and nectar feeder, was present in large numbers visiting the *Wahlenbergia* flowers in company with *Ceratina* sp. H (Anthophoridae), which was in addition visiting *Lobelia linearis*. *Ceratina* sp. H. was recorded in the Clanwilliam and Citrusdal districts visiting the flowers of *Aspalathus spinescens* (Papilionaceae) and the shallowly campanulate flowers of *Wahlenbergia annularis*. Additional visitors, present in smaller numbers, were *Masarina mixta*, *Ceratina* sp. J, *Ceratina* sp. K, and *Capicola* sp. C, which primarily visits *W. annularis*. Also represented in the complex of visitors was the honeybee *Apis mellifera*, which was otherwise commonly visiting *Paranomus bracteolaris*, *Homeria* sp., and *Wachendorfia* sp.

Of all these visitors the only one which was able to insert itself into the flowers was *Quartinioides* sp. N. As this insect in addition is a dependable visitor, apparently visiting only *Wahlenbergia* species, it seems likely that it should be considered the most important potential pollinator.

### *Microcodon sparsiflorum*

*Microcodon sparsiflorum* is a low-growing annual herb, much-branched from the base. It was investigated for flower visitors during the first week of October at a site 5 km to the west of Clanwilliam in an area of fynbos where it was in full flower in clearings between bushes. Also in flower at this site were *Aspalathus spinescens* (Papilionaceae) and various species of Asteraceae.

The flowers of *M. sparsiflorum* are presented in clusters. The corolla, which is deeply campanulate, is "two-tone" bluish violet. There is no distinct collar of pollen-supporting hairs. Instead, the whole of the upper half of the style and the nonreceptive outer surfaces of the stigmatic lobes are densely and uniformly covered with stiff, pollen-supporting hairs. Thus a relatively long pollen column is presented.

*Microcodon sparsiflorum* was being visited solely by pollen wasps. Those captured entering flowers were *Quartinia parcepunctata* and *Quartinia persephone*. *Celonites* were in addition observed entering flowers. *Celonites bergenwahliae* was captured on the ground among the *M. sparsiflorum* plants and it is therefore highly probable that it was this species of *Celonites* that was seen to be visiting the flowers. *Q. parcepunctata* was considered the most important potential pollinator of *W. paniculata*. *Quartinia* species, however, seem to be rather small to be the pollinators of the larger-flow-

ered *M. sparsiflorum*, and it seems likely that *Celonites*, which have a better flower fit, are the more important potential pollinators. It is probable, however, that *Quartinia* species are important pollinators when the flowers are small as a result of there having been insufficient water when the plants were growing.

## Evaluation

In the southwestern Cape it was found that the deeply campanulate *Wahlenbergia* species are predictably visited by one or more species of masarine but that the shallowly campanulate *Wahlenbergia annularis* is rarely visited by masarines. Conversely, the shallow-flowered species is predictably visited by large melittid bees, *Capicola* spp., which very rarely visit the deep-flowered species and then only casually. The melittid bee *Haplomelitta ogilviei*, only males of which have been recorded from *W. annularis*, is considered to be a casual visitor to *Wahlenbergia*. This is reinforced by the observations concerning it as a dependable visitor to *Monopsis debilis* growing in close proximity to *Wahlenbergia*. *M. debilis* (as *M. simplex*) has furthermore been recorded as the source of provision of *H. ogilviei* by Rozen (1974), who investigated nests of this melittid at Veldrif to the southwest of Citrusdal. A small melittid bee, *Capicola* sp. E, has been collected from the deep-flowered *Wahlenbergia prostrata*, and it seems that it is most probably an expected visitor to this species at least. Other recorded insect visitors to *Wahlenbergia*—anthophorids, bombyliids, sphecoids, eumenines, and lepidopterans—are opportunists.

Very few records of insect visitors to *Wahlenbergia* in the eastern Cape have been assembled. As yet no pollen wasps or melittids have been recorded. All visitors have been opportunists, the most common being *Ceratina* species.

It is suggested that the deeply campanulate *Wahlenbergia* and *Microcodon* flowers are primarily masarine flowers and the shallowly campanulate *Wahlenbergia* flowers are primarily melittid flowers. This partitioning seems to be governed by the behavior of the insects in relation to the structure of the flowers. In the deep-flowered species the nectaries are not covered and the nectar is thus readily accessible to pollen wasps, which alight on an outwardly curved corolla lobe and enter with the dorsal surface toward the center of the flower (Plate 20). In the shallowly campanulate flowers the nectaries are protected by the expanded bases of the

filaments. A pollen wasp alighting on an outwardly curved corolla lobe and entering with its dorsal surface toward the center of the flower would have difficulty in obtaining access to the nectar. The melittid bees enter the flowers with their ventral surfaces toward the center of the flower and close to the style (Plate 21), positioned in such a way that they can readily obtain nectar from beneath the expanded filament bases.

It is concluded on the basis of behavior in the flowers, flower fit, and dependability that, in the western Cape, pollen wasps are the most important potential pollinators of deep-flowered *Wahlenbergia* species and melittids of the genus *Capicola* are the most important potential pollinators of the shallowly campanulate *Wahlenbergia annularis*.

### *Scrophulariaceae*

The family Scrophulariaceae consists of about 190 genera and 4,000 species. It is cosmopolitan but is most diverse in temperate regions and on tropical mountains (Cronquist 1981). Over 2,000 species are found in Africa. The flowers are bisexual and range from sub-actinomorphic to markedly zygomorphic. Various accounts have been given of pollination syndromes within the Scrophulariaceae (Faegri and van der Pijl 1979), the most often associated with Scrophulariaceae being that of the melittophilous gullet flowers. In North America studies made of the pollination of *Penstemon* species are of particular relevance to the present discussion, as there is a close association between some violet-flowered species of this genus and masarines of the genus *Pseudomasaris* (Torchio 1974). Little has been recorded concerning insect visitors to the flowers of Scrophulariaceae in southern Africa. The notable exception is the work on the oil-producing, spurred flowers of *Diascia* species, with which are associated bees of the genus *Rediviva* (Melittidae) (Vogel 1954; Vogel and Michener 1985; Whitehead et al. 1984; Whitehead and Steiner 1985; Steiner and Whitehead 1988; Manning and Brothers 1986).

Three genera, *Aptosimum*, *Peliostomum*, and *Polycarena sensu lato*, have been recorded as being visited by pollen wasps (Appendices 1 and 2). Whereas the associations between pollen wasps and *Polycarena sensu lato* are casual, those with *Aptosimum* and *Peliostomum* are close.

*Aptosimum* and *Peliostomum* are endemic to Africa. They are mainly southern African and, though widespread in this region, are concentrated in the western dry regions (Dyer 1975). There are about 20 known species

of *Aptosimum* and about seven known species of *Peliostomum*. They are prostrate or densely tufted, wiry herbs or undershrubs, usually with a deep taproot. The flowers, which are gullet flowers, are bluish violet or purplish violet.

Solely on the basis of corolla structure, gullet, and the color, violet, Vogel (1954) hypothesized that *Aptosimum* and *Peliostomum* are melittophilous. In the present study four species of *Aptosimum* and two species of *Peliostomum* were observed for flower visitors. Preliminary observations on the relationship between masarines and *Aptosimum* and *Peliostomum* have been published (Gess and Gess 1989).

The flowers (Figs. 59, 60, Plate 22, 23, 24) are presented with the long axis subhorizontal. The corolla is very narrow in the basal region, protecting the nectaries from all but long-tongued or minute visitors. The greater part of the corolla tube is wider but the lower surface is inwardly saccate, so all but the smallest visitors must push their way into the flower. There are four stamens in two pairs, a pair with relatively long filaments and a pair with relatively short filaments. The shorter pair of stamens is sterile in some species of *Aptosimum*. The anthers are adpressed in pairs and positioned dorsally in the flower. The style is positioned in a dorsal groove. In a freshly opened flower the stigma barely projects at the mouth of the corolla, but with time the style elongates and curves downward.

In order to be an effective pollinator of these flowers, an insect visitor must be able to enter the flower but be large enough to receive a pollen load. Such an insect requires to have a "tongue" of sufficient length to reach the nectar at the base of the narrow inner portion of the corolla tube. It is likely that a visitor is required to trigger the dehiscence of the anthers. An insect filling these requirements would, when coming from a flower from which it had received a dorsal coating of pollen (Fig. 58) and entering a flower with a downwardly presented stigma, transfer pollen to it.

### *Aptosimum procumbens*

*Aptosimum procumbens* (Fig. 59, Plates 22, 23), a prostrate, much-branched, woody perennial, forms mats of 300 mm or more during periods of years with good rains but dies back in drought years. The corolla is bluish purple with a white throat and with each of the free lobes marked with darker violet at its base. Flowering time is synchronized with rain and may be at its height in early or late summer.





Figure 58. *Celonites peliostomi*: dorsal view of posterior end of thorax and anterior end of abdomen, showing deposition of pollen ( $\times 30$ ) (top); boxed area  $\times 150$  (bottom).

*A. procumbens* was observed for flower visitors from October to December and in March at several sites in a karroid area to the northwest of Grahamstown. The most abundant and regular visitor was a masarine *Celonites clypeatus*, which was furthermore found to be carrying pure *A. procumbens* pollen in its crop. Less abundant were another masarine, *Quartinioides tarsata*, and an anthophorid, *Ceratina* sp. F. Uncommon and apparently casual visitors were a halictid, *Pachynomia glabiventris*, and a tiphiid.





Figure 59. (a) *Aptosimum procumbens* (Scrophulariaceae), longitudinal section of flower; (b) profile of *Celonites clypeatus* (legs and wings omitted) to demonstrate wasp/flower fit.

*Celonites clypeatus* appears to be restricted in its choice of flowers, having otherwise been collected from flowers only of *Aptosimum* and *Peliostomum* species at Twee Rivieren in the southern Kalahari and near Springbok in Namaqualand. It is therefore a predictable visitor to *Aptosimum* and *Peliostomum* within its distribution range. In body size it fits the corolla snugly and its tongue, 5.8 mm long, is ideally suited to reaching nectar at the base of the narrow portion of the corolla, 5 mm long (Fig. 59). *C. clypeatus* is clearly an ideal potential pollinator of *A. procumbens*.

*Quartinoides tarsata* is less restricted, having been collected not only from the flowers of *Aptosimum* and *Peliostomum* but also from flowers of Aizoaceae and Asteraceae. Furthermore, its small size makes it possible for it to come and go from the flowers without receiving a pollen load or brushing against the stigma. It is thus an expected visitor but is not likely to be an effective potential pollinator.

*Ceratina* sp. F is similar in body size to *Celonites clypeatus* and is also long-tongued. It, however, visits a relatively wide range of plant taxa, having been recorded in the Grahamstown district from flowers of Asteraceae, Aizoaceae, Selaginaceae, and Campanulaceae and in the Clanwilliam district from Papilionaceae. *Ceratina* sp. F is thus an unreliable visitor to *A. procumbens*, and although it would be possible for it to pollinate the flowers it is too unpredictable to be considered as an important potential pollinator.

### *Aptosimum spinescens*

*Aptosimum spinescens* is a much-branched, spiny shrublet. The flowers are purplish violet with a dark purple marking centrally on each corolla lobe at the mouth of the corolla tube. Leading into and down the corolla tube from these purple markings are purple stripes on white. Flowering time is synchronized with rain and may be at its height in early or late summer.

The flowers of *A. spinescens* were observed for flower visitors in the Goegab Nature Reserve and at Voëlklip, Springbok, in Namaqualand during the first three weeks of October and at Twee Rivieren in the southern Kalahari during the second week of March.

At Voëlklip the flowers were being visited solely by *C. peliostomi* and in the Goegab Nature Reserve by two *Celonites* species, *C. peliostomi* and *C. andrei*. During an uninterrupted period of observation in Goegab from 10:30 to 11:30 on October 20, 1987, 12 instances of *Celonites* entering the flowers were recorded. The only other insect which approached the flowers was an anthophorid, *Amegilla niveata*, which was too large to enter but momentarily hovered at the mouth of a flower. Of the voucher specimens taken randomly, eight were of *C. peliostomi* and only one was of *C. andrei*. Pollen from the crop of a female *C. peliostomi* was examined and was found to be solely of pollen matching that of *A. spinescens*.

At Twee Rivieren the flowers were being visited most regularly and abundantly by the same two species of *Celonites*, *C. peliostomi* and *C. andrei*. One visit by a halictid, *Nomioides* sp. A, was recorded. This bee was otherwise commonly visiting *Deverra aphylla* (Apiaceae).

*Celonites peliostomi* appears to be narrowly restricted in its choice of flowers, having otherwise been collected only from flowers of *Aptosimum indivisum* and *Peliostomum virgatum* at Voëlklip and in the Goegab Nature

Reserve, and from *P. virgatum* at Anenous and in the Nieuwoudtville district. It is therefore an expected and dependable visitor to *Aptosimum* and *Peliostomum* within its distribution range. In the Goegab Nature Reserve, where *A. spinescens*, *A. indivisum*, and *P. virgatum* were all flowering at the same time, mixed visits did not appear to be being made, as the three flower species grow in different situations. In body size *C. peliostomi* fits the corolla of *A. spinescens* snugly and its tongue, 4.8–5.0 mm long, is ideally suited to reaching nectar at the base of the narrow portion of the corolla, 4.5 mm long. *C. peliostomi* is clearly an ideal potential pollinator of *A. spinescens*.

### *Aptosimum indivisum*

*Aptosimum indivisum* is a densely tufted, long-leaved species\* with bluish violet flowers. It was observed for flower visitors at Voëlklip and in the Goegab Nature Reserve during the same periods that observations were made on *A. spinescens* and *P. virgatum*. Its only visitor was *Celonites peliostomi*, the same species as was the most common visitor to *A. spinescens* and *P. virgatum*. It was, however, most abundantly visited between 14:00 and 15:00, when visits to *P. virgatum* were almost over. Again flower fit makes *C. peliostomi* an ideal potential pollinator.

### *Aptosimum* sp. K

*Aptosimum* sp. K is a nonspiny shrublet. On opening the corolla is bluish violet with a white throat and very little, if any, sign of darker "honey guides" on the free lobes. As the day advances marked "honey guides" develop and later still they become obscured by the darkening of the throat. Each flower lasts only one day.

The flowers were observed for insect visitors at Twee Rivieren and at Kakamas during the second week of March. Insect visitation started only after the appearance of the "honey guides" but was at no time abundant. At Twee Rivieren two hymenopterans were recorded, a masarine, *Celonites clypeatus*, and an andrenid, *Meliturgula* sp. B. At Kakamas the observations were made only in the morning before the "honey guides" had developed and in the afternoon after the flowers had darkened and were beginning to fall. No insects were visiting in the morning and in the afternoon *Meliturgula* sp. B and monkey beetles were entering the flowers.

*Celonites clypeatus* in body size and tongue length is well suited to be a

potential pollinator. The nature of the visits by *Meliturgula* are unclear. Of note is that these are short-tongued bees.

### *Peliostomum virgatum*

*Peliostomum virgatum* (Figs. 60d and e, Plate 24) is a sticky, pubescent, stringy herb bearing flowers abundantly on upright stems. The corolla is purplish violet and sticky. The free lobes are, at their bases, marked laterally with white and centrally with purple.

The flowers were observed for flower visitors at several sites in the Nieuwoudtville district during the first week of October, at Anenous during the second week of October, and at several sites in the Springbok district, in particular the Goegab Nature Reserve and at Voëlklip, during the first three weeks of October. They were being visited very abundantly and regularly at all the sites by *Celonites peliostomi* and in addition occasionally by *C. andrei* and *C. clypeatus* in the Goegab Nature Reserve and by *Quartinioides tarsata* at Anenous. The pollen contents of the crop of a female *C. peliostomi* foraging on *P. virgatum* was examined and found to be all of one type matching that of *P. virgatum*. As already stated, although *C. peliostomi* at the Goegab Reserve also visits *A. spinescens* and *A. lineare*, mixed visits did not appear to be being made, as the three flower species grow in different situations.

All three species of *Celonites* have a good flower fit with respect to body size and tongue length and all are expected visitors. All are therefore potential pollinators of *P. virgatum*. *C. peliostomi*, however, seems to be the most commonly associated species.

*Quartinioides tarsata* is not restricted to the flowers of *Aptosimum* and *Peliostomum*, having been recorded also from flowers of Aizoaceae and Asteraceae. Furthermore, its small size makes it possible for it to come and go from the flowers neither receiving a pollen load nor brushing against the stigma. It is thus an expected visitor but is not likely to be an effective potential pollinator.

Struck (1990 and 1994) also recorded visitors to *P. virgatum*. In addition to visits from *Celonites peliostomi* he recorded visits by two anthophorids, *Anthophora diversipes* and *Amegilla niveata*, and a visit by a megachilid, *Megachile frontalis*. The bodies of these bees are too large for them to be inserted into the corolla, and although their tongues are long they are not long enough to be able to reach the nectar source.

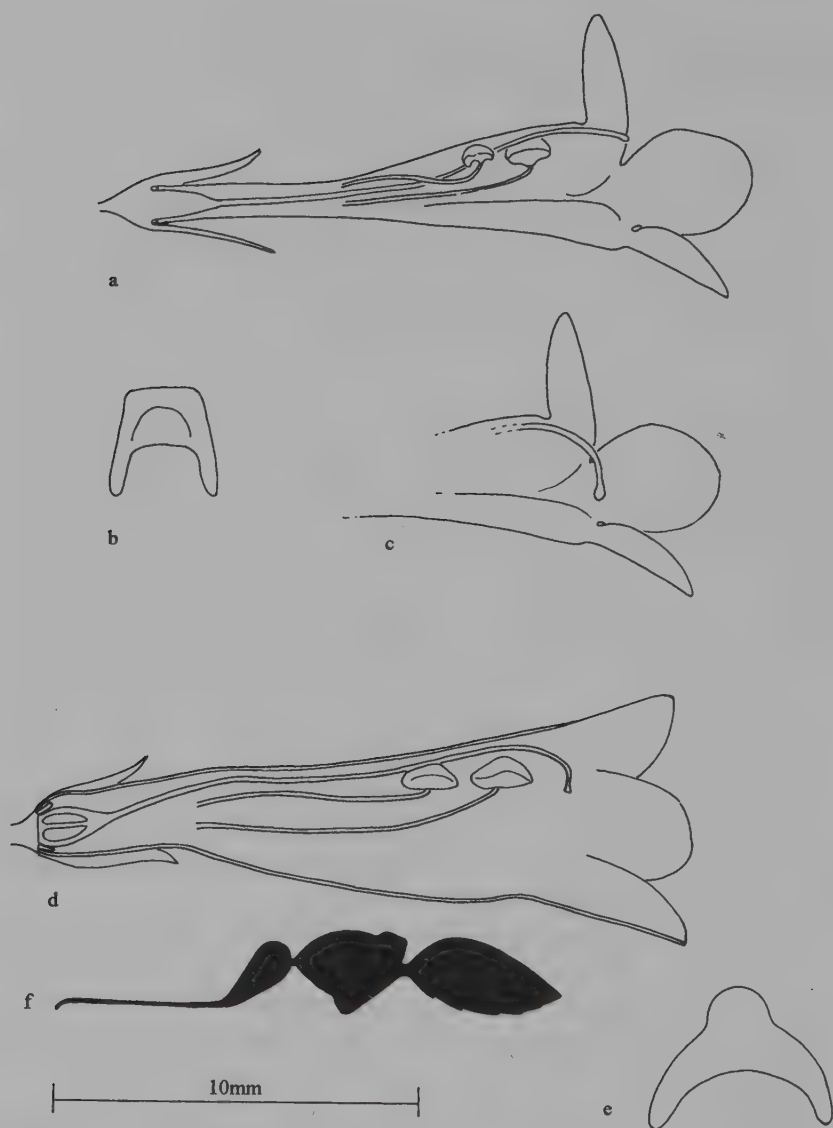


Figure 60. At top, views of *Peliostomum leucorrhizum* (Scrophulariaceae) flower: (a) longitudinal section before style elongation; (b) cross section, to show ventral invagination; (c) partial longitudinal section after style elongation. Below, views of *Peliostomum virgatum* (Scrophulariaceae) flower: (d) longitudinal section; (e) cross section, to show ventral invagination. At bottom (f) profile of *Celonites peliostomi* (legs and wings omitted) to demonstrate wasp/flower fit.



*Peliostomum leucorrhizum*

*Peliostomum leucorrhizum* (Figs. 60a–c) is a much-branched shrublet with strikingly pale grey to whitish stems. The flowers are bluish violet and markedly smaller than those of *P. virgatum* and the *Aptosimum* species considered here.

Flower visitors to *P. leucorrhizum* were observed at Williston in late September and at Kakamas and Twee Rivieren in early March. The most abundant and regular visitor at all three sites was *Quartinioides tarsata*. Three further species of *Quartinioides* were visiting in company with *Q. tarsata* at Twee Rivieren. They were, however, far less abundant.

Despite the fact that *Quartinioides tarsata* is not restricted to *Aptosimum* and *Peliostomum*, it appears to be the most likely potential pollinator of *P. leucorrhizum*. The flowers of *P. leucorrhizum* are not visited by *Celonites* species, which, because of their size, would not be able to gain entry. *Q. tarsata* gives a very good fit. When it is in position in the flower to take nectar, the length of the tongue equals that of the narrow inner portion of the corolla tube, 5.8 mm, and the waist between the thorax and the abdomen comes beneath the anthers.

## Evaluation

Pollen wasps were the principal visitors to the *Aptosimum* and *Peliostomum* species investigated. It is concluded that on the basis of behavior in the flower, flower fit, and dependability, the masarines of the genus *Celonites* are the most important potential pollinators of *A. procumbens*, *A. spinescens*, and *P. virgatum* and are probable potential pollinators of *A. lineare* and *A. sp. K.*

Furthermore, on the basis of flower fit *Quartinioides tarsata* appears to be the most important potential pollinator of *P. leucorrhizum*, the flowers of which are too small to admit the *Celonites* species. *Q. tarsata* is not, however, as dependable as the *Celonites* species associated with *Aptosimum* and *Peliostomum*, as it appears to be less restricted in its choice of flowers.

## Discussion

Insect "pollination syndromes" have been defined (for example: Baker and Hurd 1968; Faegri and van der Pijl 1979; Whitehead et al. 1987; and Vogel 1954). Accepted categories are: melittophily (bee and bee fly polli-

nation, to which should be added some tabanids); myrmecophily (ant pollination); vespiphily (wasp pollination); myiophily (fly pollination); cantharophily (beetle pollination); psychophily (butterfly pollination); phalaenophily (settling moth pollination); rhinomyiophily (long-proboscid fly pollination); sphingophily (hovering moth pollination); sapromyophily (carrion flower pollination). These have been formulated by considering the characteristics of the whole complex of flowers visited by the categories of insects giving their names to the syndromes. Characters usually listed relate to: time of anthesis; predominant colors; presence or absence of odor; nature of odor; flower shape; flower depth; presence or absence of nectar guides; presence or absence of nectaries; position of nectaries; and nature of nectar. Owing, presumably, to the sparsity of information on flowers visited by pollen wasps, these wasps have not been mentioned in discussions of pollination syndromes.

The "pollen wasp pollination syndrome," based on the present knowledge of southern African masarines as flower visitors, is characterized as follows:

*Anthesis* As pollen wasps are all day-flying, the flowers which they visit are open in the daytime (some are diurnal, closing at night).

*Predominant colors* "Light" colored flowers—white, yellow, shades of pink (rarely puce and not red), violet (not purple and rarely blue)—are favored.

*Odor* Lightly to heavily sweetly scented flowers are favored (no pollen wasps have been recorded visiting flowers with fruity, aminoid, or putrid scents).

*Flower form* Both actinomorphic and zygomorphic flowers are included; shallow, open flowers are almost entirely excluded. A colorful corolla is present in all but the Mesembryanthema, in which it is absent but in which petaloid staminodes serve the same function. Where present the corolla parts are fused forming a tube for the greater part of their length (Asteraceae, Campanulaceae, and Scrophulariaceae), or are highly differentiated (Papilionaceae). Flowers with tubular corollas are principally small, crowded into heads (Asteraceae), or are small to medium, of moderate length, presented singly or clustered and erect (Campanulaceae) or horizontally presented gullet flowers (Scrophulariaceae);

*Nectar* Nectaries or nectar-producing tissues are present, more or less concealed, with the nectar protected from evaporation, covered by the stamens (Mesembryanthema), within the corolla tube (Asteraceae, Campanulaceae, and Scrophulariaceae), or enclosed within the petals (Papilionaceae). The nectar being protected from evaporation is relatively nonviscose and can therefore be readily imbibed through the proboscis by "sucking," unlike exposed nectar, which becomes viscose and must be "licked" (Kevan and Baker 1983).

*Nectar guides* Marked nectar guides are present in the gullet flowers.

From a consideration of the published definitions of the various insect pollination syndromes, it is clear that the "pollen wasp pollination syndrome" is not distinct but, though less broad, falls within the syndrome designated melittophily. Certainly the flowers recorded here as associated with pollen wasps were all flowers assumed by Vogel (1954) to be melitophilous. This does not, however, mean that the flowers which pollen wasps visit are necessarily equally efficiently serviced by bees and/or bee flies. Indeed, the case studies considered in this chapter make it clear that, whereas the pollen wasps visiting some flowers are members of a guild of flower visitors all of which are important potential pollinators, the pollen wasps visiting others, most notably deep-flowered *Wahlenbergia* species, *Peliostomum*, and *Aptosimum*, are probably their most important potential pollinators. It is of particular note that these flowers are all violet in color, the color which in western North America is associated with *Pseudomasaris*-pollinated *Penstemon*. Red *Penstemon* are pollinated by birds and blue *Penstemon* by bees (Torchio 1974).

When considering the relative importance of pollen wasps as members of a guild of pollinators, it seems relevant to ask whether the pollen wasps are always present in company with the other members of the guild or whether there are perhaps times or places when pollen wasps are the sole or most abundant visitors. The studies considered in this chapter have shown that indeed at certain times and places pollen wasps are the sole visitors or the most abundant visitors to many mesems of the carpet and cone flower types, to certain composites, and to certain members of the Cape Group of the Crotalariae. This would indicate that there are conditions which favor pollen wasps over the other members of the guilds. In some instances, at least, this may relate to the nature of the nesting

requirements. It is also related to the degree of specialization shown by different members of a guild. Where plants other than those investigated are in flower, the members of the guild which visit a relatively wide range of flowers may select one of these other flowers. The members of the guild, such as the pollen wasps, which visit a narrow range of flowers, are under such conditions the most dependable visitors.

As noted in the introduction to this chapter, Richards (1962), when commenting on flower visiting by masarines, stated that "it may well be possible in the future to relate the structure of some of the genera to that of the flowers they visit and to the methods they use in exploiting them." The most notable structural modification of masarines for exploiting flowers is the development of long "tongues." The present study has demonstrated that tongue length and body size can be related to the structure of the flowers visited. This is most striking when the *Celonites* species associated with *Peliostomum* and *Aptosimum* are considered. Pollen wasps are otherwise generally little modified for the exploitation of the flowers which they visit. Most of the southern African masarines have short, curved legs used in pollen collection, most notably by visitors to composite capitula and mesems of the carpet flower types. Modification of the foretarsi of *Trimeria buyssoni* for pollen collection from narrow tubular flowers of Verbenaceae has been recorded by Neff and Simpson (1985). Schremmer (1959) described button-ended pollen-collecting hairs on the frons of *Celonites abbreviatus*, but our examination of a specimen of this wasp (Gess and Gess 1989) revealed that the frons is hairy but that the hairs taper toward their tips, which are curved. It is clear from the case studies presented above that, apart from tongue length and overall body size, it is principally in behavior that pollen wasps "fit" the flowers which they visit.

In economic terms pollen wasps may not be considered to be important pollinators in that they do not, like some of the indigenous megachilids, anthophorids, and honeybees, play a role in pollinating plants of economic importance, other than rooibos tea, *Aspalathus linearis* (Gess and Gess 1994). Their role in the pollination of indigenous plants should not, however, be overlooked by those interested in the conservation of plant diversity.

## Pollen Wasps and Land Use

Considering that most species in the world are insects, it is remarkable that in the recent symposium *Biotic Diversity in Southern Africa* (Huntley 1989) insects were barely mentioned and that the chapter "Conservation status of the fynbos and karoo biomes" (Hilton-Taylor and Roux 1989) mentions only three insects, all pest species: the karoo caterpillar, *Loxostege frustalis*; the brown locust, *Locustana pardalina*; and the harvester termite, *Hodotermes mossambicus*. Is this perhaps a reflection of a prevalent apathy toward insects and a consequent lack of awareness of their presence unless they are responsible for large-scale destruction? The dawning of a general realization that most species in the world are insects is suggested by Collins (1991):

In the past five years or so the biodiversity penny has dropped, and it is not just entomologists who now know that insects rule the world, even politicians appreciate the importance of insect diversity and ecology. They are asking what can be done to maintain global biodiversity? How can it be measured? What are the threats? Where should action be taken?

In order to address such questions an intimate knowledge of the structuring of ecological systems is required. We (Gess and Gess 1993) attempted to evaluate the effects of increasing land utilization on species representation and diversity of aculeate wasps and bees in the semi-arid areas of southern Africa. The present study makes it possible to identify more specifically some of the effects of land use on masarine diversity.

Pollen wasps are particularly sensitive to habitat changes. All pollen wasps require the presence of their forage plants. As all are oligolectic or narrowly polylectic, a very limited range of plants is acceptable. No masarine is able to forage on the flowers of exotic crop plants.



Nesting success of nesters on plant stems, some *Celonites* species at least, may be adversely affected by unnaturally heavy browsing.

Ground nesters—*Ceramius*, *Jugurtia*, some *Celonites* species, and some, if not all, of the species of the *Quartinia* species group—cannot nest in soil which is subject to trampling.

Those using water for nest construction, *Ceramius*, *Jugurtia*, and *Masarina*, must nest within an energetically reasonable flying distance of the water source. The water must be clean and those species which collect water at the water's edge or from damp soil near the water's edge require there to be an undisturbed, shallowly sloping "shore."

If one considers that in addition to a sensitivity to habitat change most masarines have very limited distribution ranges, it is obvious that masarines are very vulnerable to extinction.

"Land use" in the context of this chapter is restricted in the main to agriculture—that is, stock farming and the cultivation of crops—and does not therefore include mining, transport, or habitation.

### *Historical land use*

Man as a migratory hunter-gatherer in the Karoo is considered to have lived in natural balance with the environment. Although settlements resulted in localized changes in the vegetation, which have persisted over at least 700 years (Sampson 1986), indigenous mammals were not restrained, exotic species were not introduced, crop plants were not cultivated. No domestication or herding of indigenous mammals occurred.

Herders of exotic species—sheep, goats, and cattle—entered the Karoo area from the north. The prehistory of Stone Age herders in the Cape Province is reviewed by Klein (1986). It is believed that domestic stock were introduced to the western and southern Cape at or shortly after 2,000 B.P. The best-documented stock in the western and southern Cape are sheep. Cattle occur much less often and may have been introduced somewhat later than sheep (?1,600–1,500 B.P.). Goats may have been relatively abundant in the northwestern Cape, at least after 800 B.P. At Bethelsklip in the Succulent Karoo they have been identified from between about 800 B.P. and 360 B.P. (Webley, pers. comm.). Webley (1986) postulated that the Namaquas aggregated in large groups around permanent water holes in the dry summer months and split into minimal herding units during the wet winter months. The missionary Shaw (1841) re-

ported that the Namaquas who resided in the area of the Leliefontein mission station moved seasonally between the Kamiesberg (in the Succulent Karoo) in the summer and the coastal Sandveld in the winter.

These early herders do not seem to have penetrated into the Nama Karoo to any appreciable distance to the south of the Orange River or to the north of the southern Cape. Furthermore there does not seem to have been penetration of the area by the Iron Age agropastoralists coming down the east coast from the north. It would therefore appear that this area had not been subject to grazing by exotic domestic stock before these were introduced into the area by European pastoralists in the early eighteenth century.

By the end of the nineteenth century the vast herds of naturally occurring grazing and browsing mammals had been shot out to give way to large-scale stock farming. With the introduction of bore holes and wind-mill pumps, it became possible to graze stock throughout the region on a year-round basis. This was followed by the fencing of farms in the early twentieth century.

The reduction in the numbers of indigenous large mammalian herbivores, their altered patterns of dispersion, and their replacement with domestic stock resulted in substantially altered intensities and patterns of defoliation, which must have resulted in turn in large-scale changes in the vegetation. Unfortunately, these changes are inadequately documented.

### *Present land use*

#### The Great Karoo

The Great Karoo, here taken in its widest sense to include all the karroid areas inland of the western and southern escarpments, now supports a profitable small-stock industry, which is in the main based on natural pastures.

The impact of small-stock farming on the environment is variable. Variations in rainfall and vegetation dictate different choices of breed of goats or sheep and the number of head which can be supported. Furthermore, which animals are run has a profound effect upon which plants are fed upon. Whether or not rotation is practiced and what pattern of rotation is followed further affects the vegetation. For example, in the Nama Karoo long-term experimental grazing treatments have shown that

on plots grazed in the summer only there is a marked increase in the dwarf shrub and a decrease in the grass element, whereas on plots grazed in the winter there is a marked decrease in the dwarf shrub element and an increase in the grass element (Roux and Theron 1987) (Plate 25). Furthermore, drought may cause high mortality of some species, which, in the absence of continuous grazing, would re-establish after good rains. Under current grazing practices, however, local extinction of species after drought is not uncommon, resulting in possibly irreversible changes in vegetation structure and composition (Roux and Theron 1987). Many studies have aimed at assessing grazing capacities, especially since the launching of the National Grazing Strategy in 1985. Nearly all studies reflect excessive stocking rates, which, together with injudicious veld management, is the cause of widespread degradation. It has been estimated that as much as 60 percent of the veld is currently in a poor condition (Scotney 1988). The number, nature, and distribution of watering points are also variable and bring about different patterns of soil trampling. Clearly, such variations in farming practice have a profound effect on the resources available to masarines and the other aculeate wasps and bees of the communities of which they are a part.

To a limited but ever increasing extent, natural pastures are supplemented by the cultivation of lucerne pastures and lucerne hay (elsewhere known as alfalfa). Lucerne production is restricted almost entirely to the generally very limited irrigable areas along water courses, which are the favored nesting areas of *Ceramius* and *Jugurtia* species and the only areas in which sizeable nesting aggregations of some thousands of nests develop. Plowing such land clearly has a devastating effect on populations of these masarines. Smaller aggregations do build up in association with farm dams and irrigation furrows, but these are vulnerable to trampling. Furthermore, the water is liable to pollution by stock, making it unacceptable to those pollen wasps which require clean water.

### The Little Karoo

The Little Karoo, lying between the southern coastal mountains and the southern escarpment, an area of relatively high masarine species diversity (Fig. 7), is largely farmed for deciduous fruit, with the Oudtshoorn area being the center of ostrich farming. The ostriches, in the main, are pastured on lucerne lands in the irrigable river valleys. As a result, the

nesting areas of *Ceramius*, *Jugurtia*, and, in this area, *Masarina* are reduced almost entirely to isolated patches often subject to trampling. Again water is liable to pollution, making it unacceptable to pollen wasps.

### Namaqualand and the Olifants River Valley

The karroid areas to the west of the western escarpment can be divided into two regions: Namaqualand to the north of and including the Vanrhynsdorp district; and the Olifants River Valley to the south. Both are areas of relatively high masarine species diversity (Fig. 7) and endemism. Namaqualand is principally given over to small-stock farming with, to the south of Springbok, opportunistic small-scale grain production relying on winter rain. The greater area of the Olifants River Valley lies in karroid vegetation; however, the river rises in fynbos to the south in the Citrusdal district and passes through a mosaic of karroid scrub and dry fynbos in the Clanwilliam district (Moll et al. 1984). The river is strong-flowing and perennial, making the area ideally suited to irrigation farming. By 1732 European farmers were well established along the Olifants River as far north as its confluence with the Doorn River. With the construction of the Bulshoek Dam in 1922, the Clanwilliam Dam in the 1930s, and a system of canals, the valley has been intensively developed for the large-scale production of citrus fruit, deciduous fruit, vegetables, and vines. In the Vredendal district alone there are today more than 800 active land-owners involved in the State's irrigation scheme and the largest co-operative wine cellar in the southern hemisphere.

It is notable that the area around Garies in Namaqualand, previously known as a good collecting area for ground-nesting species, has in recent years been singularly unproductive. The ground has been severely damaged as a result of trampling by small stock, making nesting by ground nesters impossible. Furthermore, the species composition of the vegetation has been seriously affected, there having been a marked reduction in species diversity. The dominant plant is now *Galenia africana* (Aizoaceae). Owing to the fact that small stock do not utilize it, this plant, which is a pioneer, has increased and is now dominant in much of Namaqualand and the other semi-arid winter-rainfall areas (le Roux and Schelpe 1988).

Field experience has repeatedly demonstrated that *Galenia africana* is a plant that is unproductive of both phytophagous insects and flower-visiting insects. It would appear to be as unattractive to insects as it is to small



stock. In areas where it has become a dominant plant, there will consequently have been a reduction in population sizes of and almost certainly a reduction in species diversity of pollen wasps, indeed of insects overall. It is possible that the dramatic reduction in the populations of potentially important flower-pollinating species, such as pollen wasps and solitary bees, may result in a reduction in seed set by their forage plants and, therefore, in further loss of plant species diversity and consequently of insect diversity.

As water is required for nesting by excavators in nonfriable soil, it is relevant to consider available water sources in stock-farming areas. Naturally occurring water sources are springs, rivers, temporary pans, and temporary rainwater puddles. These are supplemented by man-made earthen dams, contour furrows, and water troughs fed from boreholes. In all instances water becomes unavailable if it is heavily polluted by drinking stock. Only species which alight on the water's surface are able to make use of water sources with steep sides. The impact on masarines of water use in stock farming is variable. Some practices have a negative effect and some a positive effect. Man's actions can cause marked temporary increases or decreases in population size. For example, the construction of a small earthen dam in the Clanwilliam district resulted in the growth over a number of years of a large aggregation of thousands of nesting *Ceramius socius*, whereas the subsequent destruction of this dam resulted in a dramatic reduction in the size of this localized population.

Crop production results in a complete change in the available resources. The soil structure and the plant cover of cultivated land are clearly different from those of uncultivated land. Where crops are farmed under irrigation, water sources are modified by changing water flow of rivers and by damming and furrow construction. The impact that cultivation will have on total species diversity clearly depends upon how extensive the cultivation is and how widespread the affected species are.

In those areas where patchy, dry-land cultivation is practiced, there is a mosaic of natural communities, cultivated areas in which the vegetation has been replaced by exotics and from which the insects have been in the main excluded by the destruction of their habitats, and fallow land with a small number of pioneer plants and the insects associated with them.

Dry-land cropping is mainly practiced in the winter-rainfall areas, in particular south of Springbok in Namaqualand and to the west of the Olifants River Valley. Extensive areas have been ploughed for the oppor-



tunistic production of wheat. Replacement of the species-rich vegetation with a single graminaceous species results locally in almost total insect species loss. When such lands are left fallow or abandoned, pioneer plants come in. Initially a limited range of annuals predominate, often forming almost pure stands. These annuals are species which are present but uncommon in the species-diverse communities of the surrounding undisturbed areas. An increase in population size of the insect species associated with these plants and a decrease in species diversity as compared with that of the surrounding areas results. This effect is strikingly demonstrated by the wasp and bee species associated with a complex of sympatrically occurring *Wahlenbergia* species. A number of species with deep flowers are principally visited by several species of Masarinae, whereas a shallow-flowered species *W. annularis* is principally visited by two species of Melittidae. Areas in which the deep-flowered *Wahlenbergia* species were formerly abundant and *W. annularis* was uncommon have been cultivated and then allowed to go fallow. In these areas *W. annularis* is now the dominant plant, which has resulted in the masarines being displaced and the melittids having become unnaturally abundant. As on overgrazed land in this area, the first perennial colonizer is *Galenia africana*. This rapidly becomes the dominant species, resulting in a further change in insect representation.

In the Olifants River Valley, where crops are farmed under irrigation, cultivated land is concentrated on the old flood plains and immediately adjacent areas. As water is available throughout the year, planting time, growing period, and success of fertilizer application are not limited by timing and amount of rain. This results in an intensive and continuous use of land for crop production. The use of ever larger, multi-span, self-propelled overhead sprinklers has resulted in ever larger lands under cultivation and a consequent continuing loss of unploughed land.

The areas most suited for large-scale cultivation are the same areas which are, due to the availability of water, particularly suited for intensive nesting by masarines, indeed by a wide range of aculeate wasps and bees. Ploughing, vegetation clearing and replacement with a limited range of crop plants, most of which are exotics, and application of "artificial out of season rain" result in localized extermination of entire communities. The extent of the cultivated areas and of the distribution ranges of the aculeate wasps and bees will govern the overall extent of this loss. Where there is rapid expansion of land under cultivation and where there is a high

incidence of endemism, as with the pollen wasps, multiple species loss is anticipated. Five species of *Ceramius* with limited distributions centered on this area immediately come to mind. One of these five species is *C. metanotalis*, which, though it forages on a relatively widespread plant, *Athanasia trifurcata*, is only known to nest in a limited area on the slopes above the Olifants River between Clanwilliam and Klawer. The area has been ploughed in strips. The forage plants remain on the unploughed strips. The wasps nest on the access road and forage along the strips. Elsewhere along the river, fields are ploughed without strips. Should there be a change to such a ploughing pattern, *Ceramius metanotalis* would be endangered.

Pollen wasps forage beyond the limits of their nesting sites. It is therefore possible to have a situation where, in an intensively cultivated area, suitable nesting sites for some species may remain on the fringes of these areas but forage plants are no longer available. Unlike some megachilid and anthophorid bees able to forage on exotic leguminous crops, no masarine wasps transfer to crop plants.

Localized large-scale flooding of land following the damming of rivers clearly leads to localized extirpation of whole communities of bees and aculeate wasps as a result of total habitat destruction. The availability of water for nesters on the fringes of large water bodies is dependent on the nature of the terrain, inlets with gently sloping shores and still water being more suited to aculeate wasps and bees that collect water or mud than are shores subject to wavelet action. Steep-sided water bodies are unavailable to the majority of species. Furthermore, the water in irrigation canals with steep concreted sides and rapidly flowing water is not available to aculeate wasps and bees, and therefore such canals do not represent additional water sources.

### The Southwestern Cape

To the south of the Olifants River Mountains only small pockets of indigenous vegetation remain. Almost all the land between the mountains which can be plowed has been given over to agriculture, in the main to the production of wheat, grapes for wine, and deciduous fruit. Only small, isolated pockets of unploughed land remain as refuges. River valleys are to a large degree infested with exotic weed species, most notably Australian *Acacia* species and *Sesbania*. Mountain slopes in some areas have been

planted with pines and are generally increasingly subject to invasion by exotic weed species. Clearly, in the area from the Olifants River Mountains to the Cape Peninsula the future for pollen wasps is bleak. Two examples serve to illustrate this. *Ceramius caffer*, which is endemic to this area and was previously recorded from the Stellenbosch and Tulbagh areas, is now known, despite extensive search, only from Ceres and Bot River at the eastern fringe of its distribution. Similarly, *Ceramius richardsi* is only known from two widely separated localities, one in the Citrusdal district in the southern Olifants River Valley and the other in the extreme southwestern Cape at Philadelphia. Though other refuges for these two species surely exist, they are undoubtedly small in area and widely separated. As a result, these two species are highly vulnerable to extinction.

### *Conservation status*

It has been stated that conservation efforts in southern Africa, centered on the need to conserve specific threatened mammals, have been haphazard. Although plant species and vegetation types have recently become more important in assessing the efficiency of conservation systems, they have seldom featured in the motivation and management of conservation areas (Rebello 1994).

Hilton-Taylor and le Roux (1989) reviewed the conservation status of the Fynbos and the Karoo, the main areas of distribution of the pollen wasps. They established that of the five Veld Types described by Acocks and included by them in the Fynbos, from less than 1 to 26 percent is conserved and that of all the Veld Types of the Karoo Biome, 21 occurring in the Nama Karoo and seven in the Succulent Karoo, excepting three, less than 1 percent is conserved. Six Veld Types have no portions conserved in state, semi-state, or private conservation areas. The siting of many reserves has generally been purely opportunistic or arbitrary, without regard to the distribution of plant endemics and threatened taxa. Furthermore, most of the areas when declared as conservation areas were already degraded.

Whether or not these conservation areas include pollen wasps is purely a matter of chance.

Reduction in population size or loss of pollen wasps will inevitably result in reduction in population size or loss of dependent associates, most notably their chrysidid parasites. It should also be borne in mind that the

effects of land use that result in the decline of pollen wasps will inevitably and simultaneously be resulting in the decline of whole communities of aculeate wasps and bees of which they are a part. The number of species able to continue to make a living in man-made habitats are but a fraction of those able to survive in natural habitats.

# Summary

### Biogeography

Pollen wasps mostly favor warm to hot areas with relatively low rainfall and open, scrubby vegetation. Records are concentrated in Mediterranean and temperate to hot semi-arid areas outside the tropics. None are further north than 50°N or further south than 50°S and none are from eastern North America or eastern and southern Asia.

The tribe Gayellini is restricted to the Neotropical Region whereas the tribe Masarini is more widespread, being represented in the Nearctic, Neotropical, Palaearctic, Afrotropical, and Australian regions. Within the Masarini the subtribe Paragiina is endemic to the Australian Region. The subtribe Masarina, on the other hand, is absent from the Australian Region but is represented in the Palaearctic, Afrotropical, Neotropical, and Nearctic regions. At the generic level the Masarina of the Nearctic and Neotropical regions are distinct from each other and from those of the Palaearctic and Afrotropical regions combined. Four genera are common to the Palaearctic Region and to southern Africa within the Afrotropical Region, but there are no shared species. A fifth genus is endemic to the Palaearctic, and three further genera are endemic to southern Africa within the Afrotropical Region.

It would appear that southern Africa is the area of greatest species diversity and that in this region, at least, there is a high incidence of narrow endemism.

Whereas the adoption of provisioning with pollen and nectar by the sphecoids led to a group, the bees, which has a worldwide distribution, including a broad range of biomes, the adoption of provisioning with pollen and nectar by the vespoids led to a group, the pollen wasps, which



though present in five zoogeographical regions is within those regions markedly restricted to a narrow range of biomes.

### Flower associations

Female pollen wasps, like all nonparasitic bees, visit flowers to collect pollen and nectar for provisioning their nests, and like most nonmasarine aculeate wasps and bees, both male and female masarines collect nectar for their own nourishment.

Pollen for provisioning is ingested and carried in the crop. Generally the pollen is drawn toward the mouth by the short, curved front legs or is taken by mouth directly from the anthers.

Pollen wasps differ from the majority of wasps in that most have long tongues, some considerably longer than the length of the wasp from the frons to the tip of the abdomen. The pollen wasps, like the long-tongued bees, therefore have the potential to obtain nectar from a wider range of flower forms than do short-tongued wasps and bees.

Pollen wasps are associated with a relatively small range of the flower families visited by aculeate Hymenoptera.

Where sufficient records are available, distinct major preferences are shown between zoogeographical regions: Nearctic—Hydrophylaceae (92 percent) and Scrophulariaceae (31 percent); Afrotropical Region—Aizoaceae (45 percent), Asteraceae (41 percent), Campanulaceae (18 percent), Scrophulariaceae (13 percent), and Papilionaceae (7 percent); Australian Region—Myrtaceae (47 percent) and Goodeniaceae (47 percent). Relatedness of plant preferences between zoogeographical regions is more apparent when relatedness of plant taxa is considered. Within a region there is marked overlap in masarine generic preferences for flower families. At the specific level there is marked oligolecty and narrow polylecty.

Distribution of areas of species richness of masarines and Mesembryanthema (Aizoaceae) in southern Africa coincide strikingly. Oligolectic species, in some instances at least, are more narrowly endemic than their forage plants.

### Life history

Pollen wasps in general appear to be univoltine. The flight period in winter-rainfall areas is spring to early summer, and in areas receiving spring and autumn or summer rainfall it is early summer to late summer.

There is specific variation in mate-location strategies. Any one species may practice one or more strategies. Males search for females in the vicinity of nests, at water sources, or forage plants, or they may practice "hilltopping."

The majority of nesting studies indicate that nest construction, egg laying, and provisioning are performed by a single female per nest. Nest sharing has been alleged for two species, however.

No parasitic masarines have been recorded.

Egg laying precedes provisioning. A single egg is laid per cell, either free or glued to the cell wall.

The provision is composed of pollen and nectar and ranges from wet and sticky with no definite form to a firm "loaf." Mass provisioning appears to be the general rule.

The overwintering stage is the last-instar larva, which after it has finished feeding spins a cocoon and then enters a resting prepupal phase.

Nest-guarding behavior by males is practiced by some species but not by others.

There are no records of sleeping aggregations. Sleeping and sheltering in the nest is commonly practiced by females but seems to be rare among males. Sleeping and sheltering in flowers or on plant stems has been recorded for both females and males of several species.

## Nesting

According to species, nests are sited in the ground, in nonfriable soil or friable soil, in earthen vertical banks, on stones, or on plants.

The pollen wasps for which nesting is known almost all construct their nests in their entirety. Only one masarine is known to nest in a pre-existing cavity in which it constructs cells. No temporary nest closures are constructed.

Seven nest types can be defined:

*Nest Type 1* A multicellular subvertical burrow in horizontal to subhorizontal ground excavated by the nester, with or without an entrance turret constructed from earth extracted from within the burrow but with the excavated cells not containing constructed cells. This may be excavated with the use of water (*type 1A*) or excavated without the use of water (*type 1B*).

*Nest Type 2* A multicellular, subhorizontal burrow in vertical to subvertical ground excavated by the nester, with an entrance turret constructed from earth extracted from within the burrow, and with the walls of each excavated cell lined with cemented earth excavated within the burrow.

*Nest Type 3* A multicellular, subvertical burrow in horizontal to subhorizontal ground excavated by the nester, with or without an entrance turret constructed from earth extracted from within the burrow, and with each cell containing a constructed cell formed from earth excavated within the burrow. The main shaft may terminate in a cell (*type 3A*) or not (*type 3B*).

*Nest Type 4* A group of constructed cells attached to plant stems or stones.

*Nest Type 5* Constructed cells located in a pre-existing cavity, with soil for cell construction collected from a quarry site at some distance from the nest.

*Nest Type 6* A self-excavated, sloping burrow in friable soil with an excavated cell in which is an earthen cell constructed from soil collected from a quarry site at some distance from the nest.

*Nest Type 7* A subvertical, silk-lined burrow in friable soil, surmounted by a silk and sand turret and having an excavated cell in which is a constructed sand and silk cell.

Three bonding agents, water (Nest Types 1, 2, and 3), nectar (Nest Type 4 and almost certainly 5 and 6), and silk (Nest Type 7), are known to be used by pollen wasps in nest construction.

Nesters in nonfriable soil using water extract the soil solely by using the mandibles. In friable soil the Nest Type 1B excavators carry out soil held between the underside of the head and the prosternum, the genae being fringed with ammochaetae, and the Nest Type 6 excavator rakes out the soil with the aid of foretarsal rakes.

Discernable are a possible primary evolutionary sequence, from ground nesting to aerial nesting (Nest Type 1 → 3 → 4), and a possible secondary evolutionary sequence, a return from aerial to ground nesting (Nest Type 4 → 5 → 6).

## Associates

### ECTOPARASITES

Mites, of the family Winterschmitiidae (= Saproglyphidae), are only known to be associated with the genus *Ceramius*, in which they are restricted to species of groups 2, 3, and 6. They are apparently present throughout the life cycle of the wasps, with which their own life cycle is synchronized.

### ENDOPARASITES

Strepsiterans have been recorded as parasites of the genus *Paragia* but of no other masarines.

### "PARASITES" IN NESTS

Mutillids have been reared from the cocoons of some pollen wasps. These are not, however, specifically parasites of their hosts but rather appear to be associated with a particular ecological niche and to attack suitable host species found within that niche.

Four genera of chrysidids have been found associated with pollen wasp nests. *Allocoelia*, of the monogeneric tribe Allocoeliini, is restricted to the Afrotropical Region. Evidence suggests that it is solely associated with pollen wasps. Two genera of Chrysidini—a western North American genus, *Chrysurissa*, and a Palaearctic and Afrotropical genus, *Spintharina*—seem to be closely associated with pollen wasps. Of the large and widely distributed genus *Chrysis*, otherwise recorded from a wide range of hosts, three species have been recorded from pollen wasps.

There are a single record of an apparent association between a chalcid and *Pseudomasaris* and several records of apparent associations between gasteruptiids and *Paragia*.

The larvae of a meloid, *Ceroctis groendali* (Lyttinae: Mylabrini), feed on the provision and larvae of *Ceramius lichtensteinii*.

### NEST USURPERS

In southern Africa ground-nesting pollen wasps are subject to usurpation of nests by megachilid bees. These bees are not, however, restricted to pollen wasp nests.

## PREDATORS

There are no records of predators that prey specifically on pollen wasps. Masarines have, however, been listed as prey of sphecoids that provision with mixed hymenopteran prey. It is highly likely that they also fall prey to birds, robber flies (Asilidae), assassin bugs (Reduviidae), mantids (Mantodea), and crab spiders (Thomisidae).

## Pollen wasps as potential pollinators

An evaluation of pollen wasps as potential pollinators of their forage plants in southern Africa has shown that:

The behavior of pollen wasps on flowers of melittophilous Aizoaceae makes them efficient potential pollinators of these flowers.

The flowers of Asteraceae are serviced by guilds of potential pollinators and, where they are abundant, pollen wasps associated with Asteraceae are important members of these guilds.

The Cape Group of the Crotalariaeae is serviced by guilds of potential pollinators. Where they are abundant pollen wasps associated with these plants, in particular with *Aspalathus*, are probably important members of these guilds.

There is a strong mutualistic association between deeply campanulate *Wahlenbergia* and *Microcodon* (both Campanulaceae) flowers and certain pollen wasps but not between pollen wasps and shallowly campanulate flowers, which are associated with certain melittid bees.

There is a strong mutualistic and possibly exclusive association between certain pollen wasps and *Aptosimum* and *Peliostomum* (Scrophulariaceae).

The "pollen wasp pollination syndrome," though less broad, falls within the syndrome designated melittophily (the bee and bee fly pollination syndrome). This does not mean, however, that the flowers visited by pollen wasps are necessarily equally efficiently serviced by bees and/or bee flies. Indeed, the case studies considered make it clear that whereas the pollen wasps visiting some flower groups are members of a guild of flower



visitors, all of which are potential pollinators, the pollen wasps visiting others are probably their most important pollinators.

### Pollen wasps and land use

Pollen wasps must be subject to population reduction and ultimately species loss in areas of intensive stock farming and land cultivation resulting from:

- loss of forage plants due to overgrazing, seasonal grazing patterns that bring about changes in plant communities, and land clearing;

- destruction of ground-nesting sites by excessive trampling, tilling of the land, or flooding, and of plant-nesting sites by heavy browsing;

- unavailability of water as a result of damming, canalizing, pollution, and trampling of the "shore."



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## APPENDIX 1

### *Records of flower visiting by masarine wasps*

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The genera and species of the wasps are arranged alphabetically within geographic region. The flowers visited are presented with families, genera, and species in alphabetical order. Where source references are not given, the records are based on label data and fieldnotes in the collection of the Albany Museum, Grahamstown, South Africa, and the South African Museum, Cape Town, South Africa.

The abbreviations should be understood as follows:

Color	B = blue; C = crimson; O = orange; Pi = pink; PiR = pinkish red; Pu = purple; PuPi = purplish pink; V = violet; W = white; Y = yellow; WY = cream
Sex	F = female; FF = females; M = male; MM = males
Numbers	digits = numbers of specimens captured if recorded; m = many observations of visits to flowers; p = pollen from provision representing an unknown number of visits to flowers
Place	AUS = Australia; NA = North America; SA = South Africa

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## NEARCTIC REGION

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### *Pseudomasaris* Ashmead

#### *Pseudomasaris basirufus* Rohwer

##### Hydrophyllaceae

##### *Phacelia* Juss.

*P.* spp.

FF&MM

Western NA; from  
Richards 1963

#### *Pseudomasaris coquilletti* Rohwer

##### Hydrophyllaceae

##### *Eriodyction* Benth.

*E.* spp.

Western NA; from Cooper  
and Bequaert 1951

<i>Phacelia</i> Juss.		
<i>P. spp.</i>		Western NA; from Cooper and Bequaert 1951
<i>P. spp.</i>	FF&MM	Western NA; from Richards 1963
Onagraceae		
<i>Oenothera</i> L.		
<i>O. sp.</i>	F	Western NA; from Richards 1963
Papaveraceae		
<i>Escholtzia</i> Cham.		
<i>E. sp.</i>	M	Western NA; from Richards 1966*
Rhamnaceae		
<i>Ceanothus</i> L.		
<i>C. sp.</i>	M	Western NA; from Richards 1963
<i>Pseudomasaris edwardsii</i> (Cresson)		
Boraginaceae		
<i>Cryptantha</i> Lehm.		
<i>C. spp.</i>	FF	Western NA; from Richards 1966
Caprifoliaceae		
<i>Symphoricarpos</i> Dill. ex Jus.		
<i>S. sp.</i>	M	Western NA; from Richards 1963
Asteraceae (Compositae)		
<i>Chaenactis</i> DC.		
<i>C. sp.</i>	F	Western NA; from Richards 1963
Hydrophyllaceae		
<i>Eriodyction</i> Benth.		
<i>E. spp.</i>		Western NA; from Cooper and Bequaert 1951
<i>E. sp.</i>	FF&MM	Western NA; from Richards 1966
<i>Phacelia</i> Juss.		
<i>P. spp.</i>		Western NA; from Cooper and Bequaert 1951
<i>P. spp.</i>	FF&MM	Western NA; from Richards 1963

<i>P. spp.</i>	FF&MM	Western NA; from Richards 1966
<i>P. spp.</i>	p	Western NA; Torchio 1970
Lamiaceae (Labiatae)		
<i>Salvia</i> (Tourn.) L.		
<i>S. sp.</i>	F	Western NA; from Richards 1966
<i>Mentha</i> (Tourn.) L.		
<i>M. sp.</i>	F	Western NA; from Richards 1963
Onagraceae		
<i>Oenothera</i> L.		
<i>O. sp.</i>	F	Western NA; from Richards 1963
<i>O. sp.</i>	M	Western NA; from Richards 1966
Rhamnaceae		
<i>Ceanothus</i> L.		
<i>C. spp.</i>	M	Western NA; from Richards 1963
Tamaricaceae		
<i>Tamarix</i> L.		
<i>T. sp.</i>	F	Western NA; from Richards 1963
<i>Pseudomasaris macneilli</i> R. M. Bohart		
Hydrophyllaceae		
<i>Hydrophyllum</i> L.		
<i>H. sp.</i>		Western NA; from Richards 1963
<i>Phacelia</i> Juss.		
<i>P. sp.</i>		Western NA; from Richards 1963
<i>Pseudomasaris maculifrons</i> (Fox)		
Boraginaceae		
<i>Cryptantha</i> Lehm.		
<i>C. sp.</i>	FF	Western NA; from Richards 1963
Hydrophyllaceae		
<i>Phacelia</i> Juss.		
<i>P. spp.</i>	FF&MM	Western NA; from Richards 1963



<i>P. spp.</i>		Western NA; from Richards 1966
Loasaceae		
<i>Eucnide</i> Zucc.		
<i>E. sp.</i>	M	Western NA; from Richards 1963
Malvaceae		
<i>Sphaeralcea</i> A.St Hil.		
<i>S. sp.</i>	F	Western NA; from Richards 1963
Papilionaceae (Fabaceae)		
<i>Astragalus</i> Tourn. ex L.		
<i>A. sp.</i>	F	Western NA; from Richards 1963
Rosaceae		
<i>Prunus</i> (Tourn.) L.		
<i>P. sp.</i>	M	Western NA; from Richards 1963
<i>Pseudomasaris marginalis</i> (Cresson)		
Hydrophyllaceae		
<i>Phacelia</i> Juss.		
<i>P. spp.</i>		Western NA; from Cooper & Bequaert 1951
<i>Pseudomasaris occidentalis</i> (Cresson)		
Scrophulariaceae		
<i>Penstemon</i> (Mitch.) Smidel.		
<i>P. sp.</i>		Western NA; from Cooper & Bequaert 1951
<i>Pseudomasaris phaceliae</i> Rohwer		
Hydrophyllaceae		
<i>Phacelia</i> Juss.		
<i>P. sp.</i>		Western NA; from Cooper & Bequaert 1951
<i>P. spp.</i>		Western NA; from Richards 1966
<i>Pseudomasaris texanus</i> (Cresson)		
Hydrophyllaceae		
<i>Phacelia</i> Juss.		
<i>P. spp.</i>		Western NA; from Cooper & Bequaert 1951

*Pseudomasaris vespoides* (Cresson)

## Asteraceae (Compositae)

*Aster* Tourn. ex L.

<i>A. sp.</i>	F	Western NA; from Richards 1963
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"thistle"	F	Western NA; from Richards 1963
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## Hydrophyllaceae

*Nama* L.

<i>N. sp.</i>	F&M	Western NA; from Richards 1963
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*Phacelia* Juss.

<i>P. sp.</i>	F	Western NA; from Richards 1963
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## Lamiaceae (Labiatae)

*Salvia* (Tourn.) L.

<i>S. carduacea</i> Benth.		Western NA; from Richards 1966
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## Onagraceae

*Clarkia* Pursh.

<i>C.sp.</i>	F	Western NA; from Richards 1963
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## Papaveraceae

*Platystemon* Benth.

<i>P. sp.</i>	MM	Western NA; from Richards 1963
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## Ranunculaceae

*Ranunculus* (Tourn.) L.

<i>R. sp.</i>	FF&MM	Western NA; from Richards 1963
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## Scrophulariaceae

*Penstemon* (Mitch.) Smidel.

<i>P. spp.</i>		Western NA; from Cooper & Bequaert 1951
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<i>P. spp.</i>		Western NA; Torchio 1974
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<i>P. spp.</i>		Western NA; from Richards 1966
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<i>P. spp.</i>	FF&MM	Western NA; from Richards 1963
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*Pseudomasaris wheeleri* J. Bequaert

## Asteraceae (Compositae)

*Peucephyllum* A.Gray.

<i>P.</i> sp.	FF&MM	Western NA; from Richards 1963
<i>P.</i> sp.	FF	Western NA; from Richards 1966

## Hydrophyllaceae

*Eriodictyon* Benth.

<i>E.</i> sp.		Western NA; from Cooper & Bequaert 1951
<i>E.</i> spp.	MM	Western NA; from Richards 1966
<i>E.</i> spp.	FF&M	Western NA; from Richards 1963

## Lamiaceae (Labiatae)

*Hyptis* Jacq.

<i>H.</i> sp.	MM	Western NA; from Richards 1966
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## Liliaceae

*Yucca* Dill. ex L.

<i>Y.</i> sp.	F	Western NA; from Richards 1963
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## Scrophulariaceae

*Penstemon* (Mitch.) Smidel.

<i>P.</i> sp.		Western NA; from Cooper & Bequaert 1951
<i>P.</i> sp.	FF&MM	Western NA; from Richards 1963
<i>P.</i> sp.	FF&MM	Western NA; from Richards 1966

## Zygophyllaceae

*Larrea* Cav.

<i>L.</i> sp.	F	Western NA; from Richards 1966
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*Pseudomasaris zonalis* (Cresson)

## Asteraceae (Compositae)

*Arnica* Rupp. ex L.

<i>A.</i> sp.	F	Western NA; from Richards 1963
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<i>Encelia</i> Adans.		
<i>E. sp.</i>	F	Western NA; from Richards 1963
<i>Grindelia</i> Willd.		
<i>G. sp.</i>	F	Western NA; from Richards 1963
Hydrophyllaceae		
<i>Phacelia</i> Juss.		
<i>P. sp.</i>		Western NA; from Cooper and Bequaert 1951
<i>P. spp.</i>	FF&MM	Western NA; from Richards 1963
Ranunculaceae		
<i>Ranunculus</i> (Tourn.) L.		
<i>R. sp.</i>	F	Western NA; from Richards 1963
Rhamnaceae		
<i>Ceanothus</i> L.		
<i>C. sp.</i>	F&M	Western NA; from Richards 1963
Scrophulariaceae		
<i>Bessya</i> Rydb.		
<i>B. sp.</i>		Western NA; from Cooper & Bequaert 1951
<i>Penstemon</i> (Mitch.) Smidel.		
<i>P. sp.</i>	F	Western NA; from Richards 1963

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## NEOTROPICAL REGION

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### *Gayella* Spinola

#### *Gayella araucana* Willink

##### Apiaceae

*Homalocarpus* Hook. and Arn.

*H. dichotomus* (Poepp. ex DC.)

Math. ex Const.

F 1

Chile; Perez 1989

<i>Gayella eumenoides</i> Spinola		
Anacardiaceae		
<i>Schinus</i> L.		
<i>S. dependens</i> Ortega		Chile; Claude-Joseph 1930 in Richards 1962
Asteraceae (Compositae)		
<i>Baccharis</i> L.		
<i>B. sp.</i>		Chile; Claude-Joseph 1930 in Richards 1962
Rosaceae		
<i>Quillaja</i> Molina		
<i>Q. saponica</i> Molina		Chile; Claude-Joseph 1930 in Richards 1962
<i>Gayella reedi</i> Willink		
Papilionaceae (Fabaceae)		
<i>Adesmia</i> DC.		
<i>A. melanthes</i> Phil.	M 2	Chile; Perez 1989

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*Microtrimeria* Bequaert

<i>M. atacama</i> Fritz		
Bignoniaceae		
<i>Argylia</i> D. Don.		
<i>A. radiata</i> (L.) D. Don.	F 1	Chile; Perez 1989
Boraginaceae		
<i>Heliotropium</i> (Tourn.) L.		
<i>H. sp.</i>	M 4	Chile; Perez 1989
Malvaceae		
<i>Cristaria</i> (Heist.) Cav.		
<i>C. inconspicua</i> Phil. ex Phil.	F 1	Chile; Perez 1989

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*Trimeria* Saussure

<i>Trimeria americana</i> (Saussure)		
Boraginaceae		
<i>Heliotropium</i> (Tourn.) L.		
<i>H. vernonicifolium</i> Griseb.	F 5	Argentina; A. Willink in Neff & Simpson 1985



<i>H. veronicifolium</i>	M 2	Argentina; A. Willink in Neff & Simpson 1985
<i>Trimeria buyssoni</i> Brèthes		
Boraginaceae		
<i>Heliotropium</i> (Tourn.) L.		
<i>H. mendocinum</i> Phil.	F 1	Argentina; Neff & Simpson 1985
<i>H. mendocinum</i>	M 2	Argentina; Neff & Simpson 1985
Malvaceae		
<i>Sphaeralcea</i> A. St Hil.		
<i>S. sp.</i>	M 1	Argentina; Neff & Simpson 1985
Verbenaceae		
<i>Glandularia</i> J. F. Gmel.		
<i>G. hookeriana</i> Covash Schnack	F 9	Argentina; Neff & Simpson 1985
<i>G. hookeriana</i>	M 4	Argentina; Neff & Simpson 1985
<i>Lantana</i> L.		
<i>L. aristata</i> Briq.	F 1	Argentina; Neff & Simpson 1985
<i>Lippia</i> Hout. ex L.		
<i>L. nodiflora</i> (L.)		Argentina; Jörgenson 1912 in Bequaert 1940
<i>Verbena</i> L.		
<i>V. sp.</i>	F 2	Argentina; Neff & Simpson 1985
<i>Trimeria howardi</i> Bertoni		
Portulacaceae		
<i>Talinum</i> Adans.		
<i>T. patens</i> (Jacquin)	m	Paraguay; Bertoni 1911
<i>Trimeria monrosi</i> Willink		
Asteraceae (Compositae)		
A	F 1	Argentina; Neff & Simpson 1985
B	F 1	Argentina; Neff & Simpson 1985

## PALAEARCTIC REGION

*Celonites* Latreille*Celonites abbreviatus* (Villers)

## Boraginaceae

*Echium* Tourn. ex L.*E.* sp.

Austria; Schremmer 1959

## Crassulaceae

*Sedum* Tourn. ex L.*S. reflexum* L.Southern Germany; Friese  
cited in Blüthgen 1961*S.* sp.Southern Germany;  
Schmiedeknecht in  
Bequaert 1940

## Geraniaceae

*Erodium* L'Herit.*E. circutaria* (L.) L'HeritSouthern Germany;  
Blüthgen 1961

## Lamiaceae (Labiatae)

*Ballota* L.*B.* sp.Southern Germany; Klein  
cited in Blüthgen 1961*Calamintha* (Tourn.) Lam.*C. alpina* (L.)Italy; Loew in  
Bequaert 1940*C.* sp.Southern Germany;  
Blüthgen 1961*Origanum* Tourn. ex L.*O. vulgare* L.Southern Germany;  
Bluthgen, 1961*Prunella* L.*P. grandiflora* Jacq.Southern Germany;  
Enslin 1922 cited in  
Richards 1962*Salvia* (Tourn.) L.*S. officinalis* L.

m

Yugoslavia;  
Schremmer 1959*Thymus* Tourn. ex L.*T.* sp.Southern Germany;  
Blüthgen 1961

<i>Teucrium</i> (Tourn.) L.		
<i>T. montanum</i> L.		Southern Germany; Friese in Bequaert 1940
<i>Celonites afer</i> Lepeletier		
Apiaceae (Umbelliferae)		
<i>Bupleurum</i> (Tourn.) L.		
<i>B. maritimum</i> L.		Algeria; Dours in Bequaert 1940
Asteraceae (Compositae)		
<i>Microlonchus</i> Cass.		
<i>M. salmanticus</i> de Candolle		Algeria; Eaton in Bequaert 1940
Boraginaceae		
<i>Echium</i> Tourn. ex L.		
<i>E. confusum</i> de Coincy		Algeria; Bequaert 1940
<i>E. humile</i> Desfontaines		Algeria; Eaton in Bequaert 1940
<i>E. italicum</i> L.		Algeria; Eaton in Bequaert 1940
<i>E. sp.</i>		Morocco; Cockerell in Bequaert 1940
Lamiaceae		
<i>Teucrium</i> (Tourn.) L.		
<i>T. aurem</i> Schreber		Southern France; Bernard in Bequaert 1940
<i>Celonites cyprius</i> Saussure		
Boraginaceae		
<i>Heliotropium</i> (Tourn.) L.		
<i>H. sp.</i>	m	Cyprus; Richards 1962
<i>Celonites hystrix</i> Kostylev		
Boraginaceae		
<i>Anchusa</i> L.		
<i>A. sp.</i>		Tadjikistan; Popov 1948 in Richards 1962
<i>Celonites jousseaumei</i> Buysson		
Boraginaceae		
<i>Heliotropium</i> (Tourn.) L.		
<i>H. sp.</i>		Sudan; Richards 1962

*Celonites mayeti* Spinola (as *C. afer* Lepeletier)

Lamiaceae (Labiatae)

*Teucrium* (Tourn.) L.*T. aureum* SchreberSouthern France;  
Bequaert 1940 cited in  
Richards 1962*Celonites modestus bisinterruptus* Kostylev

Boraginaceae

*Anchusa* L.*A.* sp.Tadjikistan; Popov 1948  
in Richards 1962*Celonites octoannulatus hissaricus* Kostylev

Boraginaceae

*Anchusa* L.*A.* sp.Tadjikistan; Popov 1948 in  
Richards 1962*Celonites rugiceps* Bischoff

Boraginaceae

*Heliotropium* (Tourn.) L.*H.* sp.

m

Cyprus; Richards 1962

*Ceramius* Latreille*Ceramius* Group 1*Ceramius caucasicus* Ed. André

Plumbaginaceae

*Acantholimon* Boiss.*A. venustum* Boiss.Asia Minor; Fahringer  
1922 in Richards 1962*Ceramius fonscolombi* Latreille (as *oraniensis* Lepeletier)

Resedaceae

*Reseda* Tourn. ex L.*R.* sp.Algiers; Bequaert 1940 in  
Richards 1962*Ceramius* Group 7*Ceramius bischoffi* Richards

Papilionaceae (Fabaceae)

*Lotus* (Tourn.) L.*L.* sp.

F 1

Spain; van Heijningen in  
Richards 1963

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Apiaceae (Umbelliferae)		
<i>Oenanthe</i> (Tourn.) L.		
<i>O. lachenalii</i> C.C.	F 1	Spain; van Heijningen in Richards 1963
<i>Ceramius lusitanicus</i> Klug		
Papilionaceae (Fabaceae)		
<i>Anthyllis</i> Riv.		
<i>A. cytisoides</i> L.	M 2	Spain; van der Vecht in Richards 1962
<i>Bonjeania</i> Rchb.		
<i>B. hirsuta</i> Rchb.	M 1	Spain; van der Vecht in Richards 1962
<i>Ceramius vechti</i> Richards		
Lamiaceae (Labiatae)		
<i>Thymus</i> Tourn. ex L.		
<i>T. mastichina</i> L.	M 1	Spain; van Heijningen in Richards 1963

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<i>Jugurtia</i> Saussure		
<i>Jugurtia algerica</i> (Schulthess)		
Apiaceae (Umbelliferae)		
<i>Ammi</i> (Tourn.) L.		
<i>A. visnaga</i> Lamark		Algeria; Bequaert in Bequaert 1940
<i>Jugurtia biskrensis</i> J. Bequaert		
Apiaceae (Umbelliferae)		
<i>Ammi</i> (Tourn.) L.		
<i>A. visnaga</i> Lamark		Algeria; Bequaert in Bequaert 1940
<i>Jugurtia oraniensis</i> (Lepelletier)		
Asteraceae (Compositae)		
<i>Centaurea</i> L.		
<i>C. sp.</i>		Algeria; Schmiedeknecht in Bequaert 1940
Boraginaceae		
<i>Echium</i> Tourn. ex L.		
<i>E. sp.</i>		Algeria; Eaton in Bequaert 1940



## Convolvulaceae

*Convolvulus* (Tourn.) L.*C. arvensis* L.Algeria; Eaton in  
Bequaert 1940

## Malvaceae

*Malva* (Tourn.) L.*M. sylvestris* L.Algeria; Eaton in  
Bequaert 1940

## Scrophulariaceae

*Scrophularia* Tourn. ex L.*S. sp.*Algeria; Schmiedeknecht in  
Bequaert 1940

## Apiaceae (Umbelliferae)

*Bupleurum* (Tourn.) L.*B. maritimum* L.Algeria; Dours in  
Bequaert 1940*Daucus* (Tourn.) L.*D. setifolius* DesfontainesAlgeria; Eaton in  
Bequaert 1940

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*Masaris* Fabricius*Masaris carli* Schulthess

## Tamaricaceae

*Tamarix* L.*T. sp.*Kazakhstan; Popov 1948 in  
Richards 1962*Masaris vespiformis* Fabricius

## Boraginaceae

*Echium* Tourn. ex L.*E. sp.*Algeria; Ferton in  
Bequaert 1940*E. sp.*Egypt; Morice in  
Bequaert 1940

## Lamiaceae (Labiales)

species with long corolla

V

Palestine; Enslin in  
Bequaert 1940

*Quartinia* Ed. André*Quartinia canariensis* Blüthgen

Asteraceae (Compositae)

*Launaea* Cass.

<i>L. arborescens</i> (Batt.) Murb.	F	Canary Islands; Hohmann et al. 1993
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Boraginaceae

*Heliotropium* (Tourn.) L.

<i>H. ramosissimum</i> (Lehm.) DC.	F	Canary Islands; Hohmann et al. 1993
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Caryophyllaceae

*Polycarpaea* Lam.

<i>P. nivea</i> (Ait.) Webb	M	Canary Islands; Hohmann et al. 1993
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Frankeniaceae

*Frankenia* L.

<i>F. laevis</i> L.	FF&MM	Canary Islands; Hohmann et al. 1993
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<i>F. sp.</i>		Canary Islands; Gusenleitner 1990a
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Papilionaceae (Fabaceae)

*Ononis* L.

<i>O. cf. tournefortii</i> Coss.	F	Canary Islands; Hohmann et al. 1993
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*Quartinia cincta* Benoist

Asteraceae (Compositae)

*Anacyclus* L.

<i>A. sp.</i>		Morocco; Benoist in Bequaert 1940
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*Quartinia dilecta* Ed. André

Asteraceae (Compositae)

*Picridium* Desf.

<i>P. tingitanum</i> Desfontaines		Algeria; Eaton in Bequaert 1940
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*Quartinia guichardi* Richards

Asteraceae (Compositae)

*Asteriscus* Moench.*A. stenophyllus* (Link in Buch)

<i>O. Kuntze</i>	M	Canary Islands; Hohmann et al. 1993
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<i>A. sp.</i>	M	Canary Islands; Hohmann et al. 1993
Frankeniaceae		
<i>Frankenia</i> L.		
<i>F. pulverulenta</i> L.	FF&MM	Canary Islands; Hohmann et al. 1993
<i>F. sp.</i>	FF&MM	Canary Islands; Hohmann et al. 1993
Rubiaceae		
<i>Plocoma</i> Ait.		
<i>P. pendula</i> Ait.	FF&MM	Canary Islands; Hohmann et al. 1993
<i>Quartinia major</i> Kohl		
Asteraceae (Compositae)		
<i>Asteriscus</i> Moench		
<i>A. maritimus</i> Moench		Algeria; Eaton in Bequaert 1940
<i>Calendula</i> L.		
<i>C. sp.</i>		Algeria; Schmiedeknecht in Bequaert 1940
<i>Chrysanthemum</i> (Tourn.) L.		
<i>C. myconis</i> L.		Algeria; Bequaert in Bequaert 1940
<i>Quartinia shestakovi</i> Kostylev		
Chenopodiaceae		
<i>Horaninowia</i> Fisch. et Mey.		
<i>H. ulicina</i> Fisch. et Mey.		Samarkand; Popov 1948 cited in Richards 1962
<i>Salsola</i> L.		
<i>S. sp.</i>		Tadjikistan; Popov 1948 cited in Richards 1962
<i>Quartinia soikai</i> Richards		
Asteraceae (Compositae)		
<i>Senecio</i> (Tourn.) L.		
<i>S. sp.</i>		Iran; Gusenleitner 1973
<i>Quartinia tenerifina</i> Richards		
Asteraceae (Compositae)		
<i>Schizogyne</i> Cass.		
<i>S. sericea</i> (L.f.) DC.	F&M	Canary Islands; Hohmann et al. 1993

Caryophyllaceae		
<i>Polycarpacea</i> Lam.		
<i>P. divaricata</i> (Ait.) Poir.	F&M	Canary Islands; Hohmann et al. 1993
<i>P. nivea</i> (Ait.) Webb	F&M	Canary Islands; Hohmann et al. 1993
Frankeniaceae		
<i>Frankenia</i> L.		
<i>F. laevis</i> L.	F&MM	Canary Islands; Hohmann et al. 1993
Lamiaceae		
<i>Micromeria</i> Benth.		
<i>M.</i> sp.	F&M	Canary Islands; Hohmann et al. 1993
Rubiaceae		
<i>Plocoma</i> Ait.		
<i>P. pendula</i> Ait.	FF&MM	Canary Islands; Hohmann et al. 1993
<i>Quartinia thebaica</i> Buysson		
Asteraceae (Compositae)		
<i>Senecio</i> (Tourn.) L.		
<i>S.</i> sp.		Egypt; Morice in Bequaert 1940
<i>Quartinia tricolorata</i> G. Soika		
Asteraceae (Compositae)		
<i>Senecio</i> (Tourn.) L.		
<i>S.</i> sp.		Egypt; Morice 1900 cited in Richards 1962
<i>Quartinia tuareg</i> G. Soika		
Asteraceae (Compositae)		
<i>Senecio</i> (Tourn.) L.		
<i>S.</i> sp.		Egypt; Morice 1900 cited in Richards 1962

## AFROTROPICAL REGION

*Celonites* Latreille*Celonites andrei* Brauns

## Scrophulariaceae

*Aptosimum* Burch.

*A. spinescens* (Thunb.) Weber PuV F 1 Namaqualand SA;  
S.K.Gess

*A. spinescens* PuV F 3 Kalahari SA;  
F.W.&S.K.Gess

*Peliostomum* Benth.

*P. virgatum* E.Mey ex Benth PV F 1 Namaqualand SA;  
F.W.&S.K.Gess

*Celonites bergenwabliae* Gess

## Aizoaceae: Mesembryanthema

*Herrea* Schwant.

*H. sp. B* WY F 3 Southwestern Cape SA;  
F.W.&S.K.Gess

## Aizoaceae: non-Mesembryanthema

*Coelanthum* E.Mey. ex Fenzl

*C. grandiflorum* E.Mey. W M 1 Southwestern Cape SA;  
ex Fenzl F.W.&S.K.Gess

## Asteraceae (Compositae)

*Senecio* L.

*S. cf. arenarius* Thunb. Pi F 2 Southwestern Cape SA;  
F.W.&S.K.Gess

*S. cf. arenarius* Pi M 2 Southwestern Cape SA;  
F.W.&S.K.Gess

## Campanulaceae

*Wahlenbergia* Schrad. ex Roth

*W. cf. constricta* v. Brehmer BV F 2 Southwestern Cape SA;  
F.W.&S.K.Gess

*W. cf. constricta* BV M 7 Southwestern Cape SA;  
F.W.&S.K.Gess

*W. psammophila* Schltr. PuV F 6 Southwestern Cape SA;  
F.W.&S.K.Gess

*W. psammophila* PuV M 1 Southwestern Cape SA;  
F.W.&S.K.Gess



## Geraniaceae

*Pelargonium* L'Herit

<i>P. sp.</i>	Pi	F	1	Southwestern Cape SA; F.W.&S.K.Gess
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## Scrophulariaceae

*Polycarena* Benth.

<i>P. sp.</i>	V	F	3	Southwestern Cape SA; F.W.&S.K.Gess
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<i>P. sp.</i>	V	M	1	Southwestern Cape SA; F.W.&S.K.Gess
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*Celonites capensis* Brauns

## Asteraceae (Compositae)

*Berkheya* Ehrh.

<i>B. heterophylla</i> (Thunb.) Hoffm.	Y	F	46	Eastern Cape SA; F.W.Gess
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<i>B. sp.</i>	Y	F	1	Little Karoo SA; F.W.Gess
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*Senecio* L.

<i>S. pterophorus</i> DC.	Y	F	2	Eastern Cape SA; F.W.Gess
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## Boraginaceae

*Ebretia* P.Br.

<i>E. rigida</i> (Thunb.) Druce	BV	M	1	Eastern Cape SA; F.W.&S.K.Gess
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## Campanulaceae

*Pelargonium* L'Herit

<i>P. myrrhifolium</i> (L.) L'Herit	WR	F	11	Little Karoo SA; C.F.Jacot Guillarmod
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<i>P. myrrhifolium</i>	WR	M	1	Little Karoo SA; C.F.Jacot Guillarmod
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## Scrophulariaceae

*Phyllopodium* Benth.

<i>P. cuneifolium</i> (L.f.) Benth.	BV	F	3	Eastern Cape, SA; D.W.Gess
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*Celonites clypeatus* Brauns

## Scrophulariaceae

*Aptosimum* Burch.

<i>A. procumbens</i> (Lehm.) Steud.	BV	F	31+	Eastern Cape SA; F.W., S.K., D.W.&R.W.Gess
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<i>A. procumbens</i>	BV	M	4	Eastern Cape SA; F.W., S.K., D.W.&R.W.Gess
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<i>A. procumbens</i>	BV	F	p	Eastern Cape SA; F.W.&S.K.Gess
<i>A. spinescens</i> (Thunb.) Weber	PuV	F	1	Kalahari SA; F.W.&S.K.Gess
<i>A. spinescens</i>	PuV	M	1	Kalahari SA; F.W.&S.K.Gess
<i>A. sp.</i>	BV	F	1	Kalahari SA; F.W.&S.K.Gess
<i>Peliostomum</i> Benth.				
<i>P. virgatum</i> E.Mey. ex Benth.	PV	F	1	Namaqualand SA; F.W.&S.K.Gess
<i>P. virgatum</i>	PV	M	2	Namaqualand SA; S.K.Gess
<i>Celonites latitarsis</i> Gess				
Aizoaceae: non-Mesembryanthema				
<i>Coelanthum</i> E.Mey.				
<i>C. grandiflorum</i> E.Mey. ex Fenzl	W	M	1	Southwestern Cape SA; F.W.&S.K.Gess
Campanulaceae				
<i>Wahlenbergia</i> Schrad. ex Roth				
<i>W. psammophila</i> Schltr.	PuV	F	m	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. psammophila</i>	PuV	F	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. psammophila</i>	PuV	M	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>Celonites peliostomi</i> Gess				
Scrophulariaceae				
<i>Aptosimum</i> Burch.				
<i>A. lineare</i> Marloth & Engl.	BV	F	15	Namaqualand SA; S.K.Gess
<i>A. lineare</i>	BV	M	1	Namaqualand SA; S.K.Gess
<i>A. spinescens</i> (Thunb.) Weber	PV	F	30	Namaqualand SA; F.W.&S.K.Gess
<i>A. spinescens</i>	PV	M	1	Namaqualand SA; F.W.&S.K.Gess
<i>A. spinescens</i>	PV	F	p	Namaqualand SA; F.W.&S.K.Gess

<i>Peliostomum</i> Benth.					
<i>P. virgatum</i> E.Mey. ex Benth.	PV	F	69	Namaqualand SA; F.W.&S.K.Gess	
<i>P. virgatum</i>	PV	M	8	Namaqualand SA; F.W.&S.K.Gess	
<i>P. virgatum</i>	PV	F	p	Namaqualand SA; F.W.&S.K.Gess	
<i>P. virgatum</i>	PV	F	1	Namaqualand SA; M.Struck	
<i>P. virgatum</i>	PV	F	5	Western Escarpment SA; F.W.&S.K.Gess	
<i>P. virgatum</i>	PV	M	5	Western Escarpment SA; F.W.&S.K.Gess	
<i>Celonites promontorii</i> Brauns					
Asteraceae (Compositae)					
<i>Berkheya</i> Ehrh.					
<i>B. fruticosa</i> (L.) Ehrh.	Y	F	1	Western Escarpment SA; D.W.Gess	
<i>B. fruticosa</i>	Y	F	2	Western Escarpment SA; F.W.&S.K.Gess	
<i>B. fruticosa</i>	Y	M	1	Western Escarpment SA; S.K.Gess	
<i>B. cf. spinosa</i> (L.f.) Druce	Y	F	6	Little Karoo SA; S.K.Gess	
<i>B. sp.</i>	—	F	4	Orange Free State SA; C.F.Jacot Guillarmod	
<i>Pteronia</i> L.					
<i>P. divaricata</i> (Berg.) Less	Y	F	1	Western Escarpment SA; S.K.Gess	
<i>P. divaricata</i>	Y	M	1	Western Escarpment SA; S.K.Gess	
<i>P. divaricata</i>	Y	F	1	Western Escarpment SA; F.W.&S.K.Gess	
<i>Senecio</i>					
<i>S. rosmarinifolius</i> L.f.	Y	F	2	Little Karoo SA; F.W.Gess	
Plumbaginaceae					
<i>Limonium</i> Mill.					
<i>L. sp.</i>	V	F	2	Tankwa Karoo SA; S.K.Gess	

*Celonites wahlenbergiae* Gess

Aizoaceae: Mesembryanthema

*Herrea* Schwant.*H. sp. B*

WY

F

3

Southwestern Cape SA;  
F.W.&S.K.Gess

Aizoaceae: non-Mesembryanthema

*Coelanthum* E.Mey. ex Fenzl*C. grandiflorum* E.Mey.

ex Fenzl

W

F

3

Southwestern Cape SA;  
F.W.,S.K.&D.W.Gess*C. grandiflorum*

W

M

1

Southwestern Cape SA;  
F.W.&S.K.Gess

Asteraceae (Compositae)

*Helicbrysum* Mill.*H. sp.*

Y

F

3

Southwestern Cape SA;  
F.W.&S.K.Gess*H. sp.*

Y

M

3

Southwestern Cape SA;  
F.W.&S.K.Gess

Campanulaceae

*Microcodon* A. DC.*M. sparsiflorum* A. DC.

V

F

9

Southwestern Cape SA;  
F.W.,S.K.&D.W.Gess*M. sparsiflorum*

V

M

4

Southwestern Cape SA;  
F.W.,S.K.&D.W.Gess*Wahlenbergia* Schrad. ex Roth*W. paniculata* (Thunb.)

A.DC.

BV

F

4

Southwestern Cape SA;  
F.W.,S.K.&D.W.Gess*W. paniculata*

BV

M

5

Southwestern Cape SA;  
F.W.,S.K.&D.W.Gess*W. psammophila* Schltr.

PuV

F

26

Southwestern Cape SA;  
F.W.&S.K.Gess*W. psammophila*

PuV

M

14

Southwestern Cape SA;  
F.W.&S.K.Gess*W. psammophila*

PuV

m

Southwestern Cape SA;  
F.W.&S.K.Gess

Crassulaceae

*Crassula* L.*C. dichotoma* L.

Y&amp;O

F

2

Southwestern Cape SA;  
F.W.&S.K.Gess

Geraniaceae					
<i>Pelargonium</i> L'Herit					
<i>P. sp.</i>	Pi	F	3	Southwestern Cape SA; F.W.&S.K.Gess	
Scrophulariaceae					
<i>Polycarena</i> Benth.					
<i>P. sp.</i>	—	M	1	Southwestern Cape SA; F.W.&S.K.Gess	
<i>Celonites wheeleri</i> Brauns					
Asteraceae (Compositae)					
<i>Berkbeya</i> Ehrh.					
<i>B. cf. spinosa</i> (L.f.) Druce	Y	F	2	Southern Cape SA; F.W.&S.K.Gess	
<i>Celonites</i> sp. E					
Lobeliaceae					
<i>Lobelia</i> L.					
<i>L. linearis</i> Thunb.	Pu	F	1	Western Escarpment SA; F.W.&S.K.Gess	
<i>L. linearis</i>	Pu	M	1	Western Escarpment SA; F.W.&S.K.Gess	

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### *Ceramius* Latreille

#### *Ceramius* Group 2A

#### *Ceramius cerceriformis* Saussure

##### Aizoaceae: Mesembryanthema

##### *Aridaria* N.E.Br.

<i>A. sp.</i>	W	M	1	Southwestern Cape SA; D.W.Gess
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"mesem"	Pu	F	1	Namaqualand SA; F.W.&W.H.R.Gess
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##### *Mesembryanthemum* L.

<i>M. crystallinum</i> L.	W	—	—	Eastern Cape SA; C.F.Jacot Guillarmod
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##### *Psilocaulon* N.E.Br.

##### *P. acutisepalum* (Berger)

N.E.Br.	WPi	F	1	Namaqualand SA; F.W.&S.K.Gess
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<i>P. acutisepalum</i>	WPi	F	5	Southwestern Cape SA; D.W.Gess
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<i>P. acutisepalum</i>	WPi	M	3	Southwestern Cape SA; D.W.Gess
<i>P. acutisepalum</i>	WPi		m	Southwestern Cape SA; D.W.Gess
<i>Ceramius peringueyi</i> Brauns				
Aizoaceae: Mesembryanthema				
<i>Psilocaulon</i> N.E.Br.				
<i>P. acutisepalum</i> (Berger)				
N.E.Br.	WPi	F	18	Southwestern Cape SA; F.W.&S.K.Gess
<i>P. cf. subnodosum</i> (Berger)	Pi	F	4	Southwestern Cape SA; F.W.&S.K.Gess
N.E.Br.				
<i>P. cf. subnodosum</i>	Pi	M	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>Ceramius</i> Group 2B				
<i>Ceramius clypeatus</i> Richards				
Papilionaceae (Fabaceae)				
<i>Aspalathus</i> L.				
<i>A. linearis</i> (Burm.f.)	Y	F	5	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
Dahlgren				
<i>A. linearis</i>	Y	F&M	m	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. pulicifolia</i> Dahlgren	Y	F	29	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. pulicifolia</i>	Y	M	3	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. spinescens</i> Thunb.	Y	F	72	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. spinescens</i>	Y	M	5	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. spinescens</i>	Y	F&M	m	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. spinescens</i>	Y	F	p	Southwestern Cape SA; F.W.&S.K.Gess
<i>Ceramius richardsi</i> Gess				
Papilionaceae (Fabaceae)				
<i>Aspalathus</i> L.				
<i>A. pulicifolia</i> Dahlgren	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess

<i>A. pulicifolia</i>	Y	M	1	Southwestern Cape SA; F.W.&S.K.Gess
"legume"	—	F	1	Southwestern Cape SA; V.B.Whitehead
<i>Ceramius</i> Group ?2B				
<i>Ceramius micheneri</i> Gess				
Papilionaceae (Fabaceae)				
<i>Aspalathus</i> L.				
<i>A. pulicifolia</i> Dahlgren	Y	F	10	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. pulicifolia</i>	Y	F	2	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. pulicifolia</i>	Y	M	4	Southwestern Cape SA; F.W.&S.K.Gess
<i>A. spinescens</i> Thunb.	Y	M	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>Ceramius</i> Group 3				
<i>Ceramius braunsi</i> Turner				
Asteraceae (Compositae)				
<i>Arctotheca</i> Wendl				
<i>A. calendula</i> (L.) Levyns	Y	F	2	Southwestern Cape SA; D.W.Gess
<i>A. calendula</i>	Y	M	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>Arctotis</i> L.				
<i>A. laevis</i> Thunb.	Y	F	14	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. laevis</i>	Y	F	m	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>Athanasia</i> L.				
<i>A. trifurcata</i> (L.) L.	Y	F	63	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. trifurcata</i>	Y	F	m	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. trifurcata</i>	Y	M	1	Southwestern Cape SA; D.W.Gess
<i>Pentzia</i> Thunb.				
<i>P. sp.</i>	Y	—	1	Southwestern Cape SA; D.W.Gess

"composite"	Y	M	1	Southwestern Cape SA; D.W.Gess
"composite"	—	F	p	Southwestern Cape SA; S.K.Gess
Papilionaceae (Fabaceae)				
<i>Aspalathus</i> L.				
<i>A. spinescens</i> Thunb.	Y	F	5	Southwestern Cape SA; F.W., S.K. & D.W. Gess
<i>A. spinescens</i>	Y	M	1	Southwestern Cape SA; D.W.Gess
<i>Ceramius jacoti</i> Richards				
Asteraceae (Compositae)				
<i>Pteronia</i> L.				
<i>P. incana</i> (Burm.) DC.	Y	M	3	Little Karoo SA; C.F.Jacot Guillarmod
<i>Senecio</i> L.				
<i>S. rosmarinifolius</i> L.f.	Y	F	23	Little Karoo SA; F.W., S.K., H.W. & R.W. Gess
<i>S. rosmarinifolius</i>	Y	F	p	Little Karoo SA; S.K.Gess
<i>Ceramius nigripennis</i> Saussure				
Asteraceae (Compositae)				
<i>Arctotheca</i> Wendl.				
<i>A. calendula</i> (L.) Levyns	Y	M	1	Namaqualand SA; D.W.Gess
<i>Berkheya</i> Ehrh.				
<i>B. fruticosa</i> (L.) Ehrh.	Y	F	3	Namaqualand SA; M.Struck
<i>B. fruticosa</i>	Y	F	3	Namaqualand SA; F.W. & S.K. Gess
<i>B. fruticosa</i>	Y	M	2	Namaqualand SA; F.W., S.K. & D.W. Gess
<i>B. sp.</i>	Y	M	1	Namaqualand SA; F.W. & S.K. Gess
<i>Dimorphotheca</i> Vaill. ex Moench.				
<i>D. sinuata</i> DC.	O	F	2p	Namaqualand SA; S.K.Gess
<i>Hirpicium</i> Cass.				
<i>H. alienatus</i> (Thunb.) Druce	Y	F	1	Namaqualand SA; M.Struck

<i>H. sp.</i>	Y	F	2	Namaqualand SA; F.W.&S.K.Gess
<i>H. sp.</i>	Y	M	2	Namaqualand SA; D.W.Gess
<i>Pentzia</i> Thunb.				
<i>P. suffruticosa</i> (L.) Hutch. ex Merxm.	Y	F	3	Namaqualand SA; F.W.,S.K.&D.W.Gess
<i>Ceramius toriger</i> Schulthess				
Asteraceae (Compositae)				
<i>Athanasia</i> L.				
<i>A. trifurcata</i> (L.) L.	Y	F	1	Tankwa Karoo SA; S.K.Gess
<i>Berkhaya</i> Ehrh.				
<i>B. fruticosa</i> (L.) Ehrh.	Y	F	9	Western Escarpment SA; F.W.,S.K.&D.W.Gess
<i>B. fruticosa</i>	Y	M	7	Western Escarpment SA; F.W.,S.K.&D.W.Gess
<i>Pteronia</i> L.				
<i>P. divaricata</i> (Berg.) Less.	Y	F	5	Western Escarpment SA; F.W.,S.K.&D.W.Gess
<i>P. divaricata</i>	Y	M	7	Western Escarpment SA; F.W.,S.K.&D.W.Gess
"blue rayed"	B	M	3	Tankwa Karoo SA; C.D.Michener
<i>Ceramius</i> Group 4				
<i>Ceramius beyeri</i> Brauns				
Aizoaceae: Mesembryanthema				
<i>Sphalmanthus</i> N.E.Br.				
<i>S. cf. bijliae</i> (N.E.Br.) L.Bol.	WPi	F	1	Southwestern Cape SA; F.W.,S.K.&R.W.Gess
"mesem"	W	F	1	Eastern Cape SA; F.W.Gess

*Ceramius* Group 5*Ceramius lichtensteinii* (Klug)

## Acanthaceae

*Blepharis* Juss.

<i>B. capensis</i> (L.f.) Pers.	W	F	5	Eastern Cape SA; F.W.&D.W.Gess
<i>B. capensis</i>	W	F	5	Southern Great Karoo SA; F.W.&R.W.Gess
<i>B. capensis</i>	W	M	1	Southern Great Karoo SA; F.W.&R.W.Gess

## Aizoaceae: Mesembryanthema

*Aridaria* N.E.Br.

<i>A. sp.</i>	WY	—	—	Eastern Cape SA; F.W.&S.K.Gess
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*Mesembryanthemum* L.

<i>M. aitonis</i> Jacq.	W	—	—	Eastern Cape SA; F.W.&S.K.Gess
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*Ruschia* Schwant.

<i>R. sp.</i>	W	—	—	Eastern Cape SA; F.W.Gess
<i>R. sp.</i>	W	M	1	Eastern Cape SA; F.W.Gess
<i>R. sp.</i>	PuPi	—	—	Eastern Cape SA; F.W.Gess
<i>R. sp.</i>	PuPi	—	—	Eastern Cape SA; J.G.H.Londt
<i>R. sp.</i>	—	F	p	Eastern Cape SA; S.K.Gess

*Sphalmanthus* N.E.Br.*S. cf. bijliae* (N.E.Br.)

L.Bol.	WPi	F	m	Southern Great Karoo SA; F.W.,S.K.&R.W.Gess
<i>S. cf. bijliae</i>	WPi	M	m	Southern Great Karoo SA; F.W.,S.K.&R.W.Gess
"mesem"	PuPi	M	2	Eastern Cape SA; F.W.Gess
"mesem"	Pi	F	2	Eastern Cape SA; D.W.Gess
"mesem"	W	F	1	Eastern Cape SA; F.W.Gess



"mesem"	W	M	1	Eastern Cape SA; F.W.Gess
"mesem"	WY	F&M	m	Eastern Cape SA; F.W.&S.K.Gess
"mesem"	W	F&M	m	Eastern Cape SA; F.W.&S.K.Gess
"mesem"	Pi	F&M	m	Eastern Cape SA; F.W.&S.K.Gess
"mesem"	WPi	F&M	m	Eastern Cape SA; F.W.&S.K.Gess

## Asteraceae (Compositae)

[It was noted at the time that there were no mesems in flower.]

*Senecio* L.

<i>S. pterophorus</i> DC.	Y	F	2	Eastern Cape SA; F.W.&S.K.Gess
<i>S. pterophorus</i>	Y	M	4	Eastern Cape SA; F.W.&S.K.Gess

*Ceramius* Group 6*Ceramius caffer* Saussure

## Asteraceae (Compositae)

*Berkheya* Ehrh.

<i>B. carlinifolia</i> (DC.) Roessler	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>B. sp.</i>	Y	F	1	Southwestern Cape SA; V.B.Whitehead
<i>B. sp.</i>	Y	M	1	Southwestern Cape SA; V.B.Whitehead

*Ceramius metanotalis* Richards

## Asteraceae (Compositae)

*Athanasia* L.

<i>A. trifurcata</i> (L.) L.	Y	F	14	Southwestern Cape SA; F.W., S.K. & D.W. Gess
<i>A. trifurcata</i>	Y	M	5	Southwestern Cape SA; F.W., S.K. & D.W. Gess

*Ceramius rex* Saussure

## Asteraceae (Compositae)

*Berkheya* Ehrh.

<i>B. canescens</i> DC.	Y	F	1	Namaqualand SA; F.W.Gess
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<i>B. canescens</i>	Y	F	3p	Namaqualand SA; S.K.Gess
<i>Pteronia</i> L.				
<i>P.</i> sp.	Y	M	1	Namaqualand SA; D.W.Gess
"composite"		F	p	Namaqualand SA; S.K.Gess
<i>Ceramius</i> Group 8				
<i>Ceramius bicolor</i> (Thunberg)				
Aizoaceae: Mesembryanthema				
<i>Drosanthemum</i> Schwant.				
<i>D.</i> sp.	Pi	M	1	Western Escarpment SA; F.W.&S.K.Gess
<i>Psilocaulon</i> N.E.Br.				
<i>P. acutisepalum</i> (Berger)				
N.E.Br.	WPi	F&M	m	Southwestern Cape SA; F.W.&W.H.R.Gess
<i>P. acutisepalum</i>	WPi	F&M	m	Southwestern Cape SA; F.W.&S.K.Gess
<i>P. acutisepalum</i>	WPi	F	4	Southwestern Cape SA; F.W.&S.K.Gess
<i>P. acutisepalum</i>	WPi	M	2	Southwestern Cape SA; F.W.&S.K.Gess
<i>P. acutisepalum</i>	WPi	F	p	Southwestern Cape SA; S.K.Gess
<i>P. acutisepalum</i>	WPi	F	p	Namaqualand SA; S.K.Gess
<i>Sphalmanthus</i> N.E.Br.				
<i>S. cf. bijliae</i> (N.E.Br.)				
L. Bol.	Pi	F	1	Tankwa Karoo SA; S.K.Gess
<i>S.</i> sp.	Pi	F	1	Western Escarpment SA; F.W.&S.K.Gess
<i>S.</i> sp.	Pi	M	1	Western Escarpment SA; F.W.&S.K.Gess
"mesem"	PiVW	F	2	Tankwa Karoo SA; R.W.Gess
"mesem"		F	p	Namaqualand SA; S.K.Gess
"mesems"	W	—	—	Southwestern Cape SA; C.D.Michener

*Ceramius capicola* Brauns

Aizoaceae: Mesembryanthema

*Aridaria* N.E.Br.*A. plenifolia* (N.E.Br.)

Stearn

YW – – Eastern Cape SA;  
F.W.&S.K.Gess*Drosanthemum* Schwant.*D. floribundum* (Haw.)

Schwant.

Pi F p Eastern Cape SA;  
S.K.Gess*Mesembryanthemum* L.*M. aitonis* Jacq.W F – Eastern Cape SA;  
F.W.Gess*Mestoklema* N.E.Br.*M. tuberosum* (L.) N.E.Br.PuPi F – Eastern Cape SA;  
F.W.Gess*M. tuberosum*PuPi F – Eastern Cape SA;  
F.W.Gess*Platythyra* N.E.Br.*P. haeckeliana* (Berger)

N.E.Br.

Y F 1 Eastern Cape SA;  
S.K.Gess*Ruschia* Schwant.*R. sp.*W F 29 Eastern Cape SA;  
F.W.Gess*R. sp.*W M 51 Eastern Cape SA;  
F.W.Gess*R. sp.*W – – Eastern Cape SA;  
J.G.H.Londt*R. sp.*PuPi – – Eastern Cape SA;  
J.G.H.Londt

"mesems"

WY – – Eastern Cape SA;  
F.W.&S.K.Gess

"mesems"

W – – Eastern Cape SA;  
F.W.&S.K.Gess

"mesems"

Pi – – Eastern Cape SA;  
F.W.&S.K.Gess

"mesems"

W F 4 Eastern Cape SA;  
D.W.Gess

"mesems"

W M 5 Eastern Cape SA;  
D.W.Gess

"mesems"				m	Eastern Cape SA; F.W.&S.K.Gess
Asteraceae (Compositae)					
<i>Berkheya</i> Ehrh.					
<i>B. sp.</i>	Y	F	1		Orange Free State SA; C.F.Jacot Guillarmod
<i>Ceramius linearis</i> Klug					
Aizoaceae: Mesembryanthema					
<i>Aridaria</i> N.E.Br.					
<i>A. dyeri</i> L.Bol.	YW	F	3		Eastern Cape SA; F.W.Gess
<i>A. dyeri</i>	YW	M	5		Eastern Cape SA; F.W.Gess
<i>A. plenifolia</i> (N.E.Br.) Stearn	YW	F	4		Eastern Cape SA; J.G.H.Londt
<i>A. plenifolia</i>	YW	M	4		Eastern Cape SA; J.G.H.Londt
<i>A. plenifolia</i>	YW	F	1		Eastern Cape SA; F.W.Gess
<i>A. plenifolia</i>	YW	M	1		Eastern Cape SA; F.W.Gess
<i>A. sp.</i>	YW	F	11		Eastern Cape SA; F.W.&S.K.Gess
<i>A. sp.</i>	YW	M	10		Eastern Cape SA; F.W.&S.K.Gess
<i>Drosanthemum</i> Schwant.					
<i>D. floribundum</i> (Hw.) Schwant.	Pi	M	1		Eastern Cape SA
<i>D. floribundum</i>	Pi	F	p		Eastern Cape SA; S.K.Gess
<i>Malephora</i> N.E.Br.					
<i>M. sp.</i>	YW	F	22		Eastern Cape SA; F.W.&S.K.Gess
<i>M. sp.</i>	YW	M	44		Eastern Cape SA; F.W.&S.K.Gess
<i>Mesembryanthemum</i> L.					
<i>M. aitonis</i> Jacq.	W	F	5		Eastern Cape SA; F.W.Gess
<i>M. aitonis</i>	W	M	3		Eastern Cape SA; F.W.Gess

*Ruschia* Schwant.

<i>R. sp.</i>	PuPi	–	–	Eastern Cape SA; J.G.H.Londt
<i>R. sp.</i>	W	–	–	Eastern Cape SA; J.G.H.Londt
“mesem”	W	F	1	Eastern Cape SA; F.W.Gess
“mesem”	W	M	2	Eastern Cape SA; F.W.Gess
“mesem”	Y	F	2	Eastern Cape SA; F.W.&S.K.Gess
“mesem”	Y	M	1	Eastern Cape SA; F.W.&S.K.Gess
“mesem”	YW	F&M	–	Eastern Cape SA; F.W.&S.K.Gess
“mesem”	W	–	–	Eastern Cape SA; F.W.&S.K.Gess
“mesem”	Pi	–	–	Eastern Cape SA; F.W.&S.K.Gess
“mesems”		F&M	m	Eastern Cape SA; F.W.&S.K.Gess

*Ceramius socius* Turner

## Aizoaceae: Mesembryanthema

*Psilocaulon* N.E.Br.*P. acutisepalum* (Berger)

N.E.Br.

	WPi	F&M	m	Southwestern Cape SA; F.W.&S.K.Gess
<i>P. acutisepalum</i>	WPi	F	p	Southwestern Cape SA; S.K.Gess
<i>P. acutisepalum</i>	WPi	F	6	Southwestern Cape SA; D.W.Gess
<i>P. acutisepalum</i>	WPi	M	5	Southwestern Cape SA; D.W.Gess
“mesem”	W	F	14	Tankwa Karoo SA; F.W., S.K.&R.W. Gess

## Campanulaceae

*Wahlenbergia* Schrad. ex Roth*W. paniculata* (Thunb.)

A.DC.

V	M	1	Southwestern Cape SA; F.W.Gess
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*Jugurtia* Saussure*Jugurtia confusa* Richards

Aizoaceae: Mesembryanthema

*Drosanthemum* Schwant.*D. parvifolium* (Haw.)

Schwant.

Pi F p Eastern Cape SA;  
S.K.Gess*D. parvifolium*Pi M 1 Eastern Cape SA;  
F.W.Gess

Mimosaceae

*Acacia* Mill.*A. karroo* Hayne.Y M 1 Eastern Cape SA;  
F.W.Gess*Jugurtia braunsi* (Schulthess)

Aizoaceae: Mesembryanthema

*Drosanthemum* Schwant.*D. sp.*Pi F 13 Namaqualand SA;  
S.K.Gess*D. sp.*Pi F 5 Western Escarpment SA;  
F.W.&S.K.Gess*Herrea* Schwant.*H. sp. A*Y F 1 Western Escarpment SA;  
F.W.&S.K.Gess*H. sp.*Y F 8 Namaqualand SA;  
F.W.&S.K.Gess*Leipoldtia* L. Bol.*L. sp.*Pi F 11 Namaqualand SA;  
S.K.Gess*L. sp.*Pi M 1 Namaqualand SA;  
S.K.Gess

"mesem"

Pi F 1 Namaqualand SA;  
F.W.&S.K.Gess

"mesem"

Pi F 13 Western Escarpment SA;  
F.W.&S.K.Gess

"mesem"

W F 3 Namaqualand SA;  
F.W.&S.K.Gess

Aizoaceae: non-Mesembryanthema

*Tetragonia* L.*T. sp.*Pi F 1 Namaqualand SA;  
F.W.&S.K.Gess

Asteraceae (Compositae)					
<i>Arctotheca</i> Wendl.					
<i>A. calendula</i> (L.) Levyns	Y	F	1	Namaqualand SA; D.W.Gess	
<i>Leysera</i> L.					
<i>L. gnaphalodes</i> (L.) L.	Y	F	1	Namaqualand SA; S.K.Gess	
<i>Pentzia</i> Thunb.					
<i>P. suffruticosa</i> (L.) Hutch. ex Merxm.	Y	F	1	Western Escarpment SA; F.W.&S.K.Gess	
<i>Pteronia</i> L.					
<i>P. divaricata</i> (Berg.) Less.	Y	F	4	Western Escarpment SA; D.W.Gess	
<i>P. divaricata</i>	Y	F	1	Namaqualand SA; D.W.Gess	
<i>Senecio</i> L.					
<i>S. sp.</i>	Y	F	4	Namaqualand SA; F.W.&S.K.Gess	
<i>S. sp.</i>	—	F	1	Western Escarpment SA; F.W.&S.K.Gess	
Campanulaceae					
<i>Wahlenbergia</i> Schrad. ex Roth					
<i>W. pilosa</i> Buek	V	F	12	Namaqualand SA; F.W.&S.K.Gess	
Selaginaceae					
<i>Selago</i> L.					
<i>S. sp.</i>	W	F	2	Namaqualand SA; F.W.&S.K.Gess	
<i>Jugurtia braunsiella</i> (Schulthess)					
Asteraceae (Compositae)					
<i>Athanasia</i> L.					
<i>A. sp.</i>	Y	F	3	Namaqualand SA; F.W.&S.K.Gess	
<i>Felicia</i> Cass.					
<i>F. sp.</i>	B	F	1	Namaqualand SA; S.K.Gess	
<i>Lasiospermum</i> Lag.					
<i>L. bipinnatum</i> (Thunb.) Druce	W	M	1	Eastern Cape SA; F.W.&S.K.Gess	

<i>Pteronia</i> L.								
<i>P. cf. divaricata</i> (Berg.)								
Less.	Y	F	1	Western Escarpment SA; D.W.Gess				
<i>P. cf. divaricata</i>	Y	F	7	Western Escarpment SA; F.W.&S.K.Gess				
<i>P. cf. divaricata</i>	Y	M	2	Western Escarpment SA; F.W.&S.K.Gess				
<i>P. paniculata</i> Thunb.	Y	F	1	Eastern Cape SA; F.W.&S.K.Gess				
<i>P. sp. A</i>	Y	F	1	Namaqualand SA; S.K.Gess				
<i>Senecio</i> L.								
<i>S. burchellii</i> DC.	Y	F	1	Southwestern Karoo SA; S.K.Gess				
<i>S. rosmarinifolius</i> L.f.	Y	F	5	Little Karoo SA; F.W.&R.W.Gess				
<i>S. rosmarinifolius</i>	Y	F	p	Little Karoo SA; S.K.Gess				
<i>S. rosmarinifolius</i>	Y	F	1	Tankwa Karoo SA; F.W.Gess				
<i>Jugurtia calcarata</i> Richards								
Aizoaceae: Mesembryanthema								
<i>Psilocalon</i> N.E.Br.								
<i>P. acutisepalum</i> (Berger)	WPi	F	1	Namaqualand SA; F.W.&S.K.Gess				
N.E.Br.								
<i>Jugurtia duplicata</i> Richards								
Aizoaceae: Mesembryanthema								
<i>Drosanthemum</i> Schwant.								
<i>D. sp.</i>	Pi	F	1	Western Escarpment SA; F.W.&S.K.Gess				
"mesem"	W	F	2	Western Escarpment SA; F.W.&S.K.Gess				
"mesem"	PuPi	F	1	Western Escarpment SA; F.W.&S.K.Gess				
Asteraceae (Compositae)								
<i>Pteronia</i> L.								
<i>P. cf. divaricata</i> (Berg.)								
Less.	Y	F	2	Western Escarpment SA; D.W.Gess				

*Jugurtia polita* Richards

## Asteraceae (Compositae)

*Leysera* L.

<i>L. gnaphaloides</i> (L.) L.	Y	M	6	Western Escarpment SA; F.W.&S.K.Gess
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*Osteospermum* L.*O. oppositifolia* (Ait.)

T.Norl.	Y	F	3	Western Escarpment SA; F.W.&S.K.Gess
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*Senecio* L.

<i>S. prob. nivea</i> Less	W	M	1	Western Escarpment SA; F.W.Gess
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<i>S. sp.</i>	—	M	1	Eastern Cape SA; O.W.Richards in Richards 1962
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*Jugurtia turneri* (Schulthess)

## Asteraceae (Compositae)

*Athanasia* L.

<i>A. trifurcata</i> (L.) L.	Y	F	3	Tankwa Karoo SA; S.K.Gess
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<i>A. trifurcata</i>	Y	M	1	Tankwa Karoo SA; S.K.Gess
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<i>A. trifurcata</i>	Y	F	1	Tankwa Karoo SA; R.W.Gess
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<i>A. trifurcata</i>	Y	M	1	Tankwa Karoo SA; R.W.Gess
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<i>A. sp.</i>	Y	F	3	Tankwa Karoo SA; F.W.Gess
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<i>A. sp.</i>	Y	M	1	Tankwa Karoo SA; F.W.Gess
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<i>A. sp.</i>	Y	F	1	Tankwa Karoo SA; H.W.Gess
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<i>A. sp.</i>	Y	M	1	Tankwa Karoo SA; H.W.Gess
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*Senecio* L.

<i>S. rosmarinifolia</i> L.f.	Y	F	1	Tankwa Karoo SA; F.W.Gess
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<i>S. rosmarinifolia</i>	Y	M	1	Tankwa Karoo SA; F.W.Gess
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*Jugurtia* sp. C.

Asteraceae (Compositae)

*Leysera* L.

<i>L. gnaphaloides</i> (L.) L.	Y	M	2	Western Escarpment SA; F.W.&S.K.Gess
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"composite"	Y	F	1	Western Escarpment SA; F.W.&S.K.Gess
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*Masarina* Richards*Masarina familiaris* Richards

Papilionaceae (Fabaceae)

*Aspalathus* L.

<i>A. divaricata</i> Thunb.	Y	M	1	Southwestern Cape SA; S.K.Gess
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*A. linearis* (Burm.f.)

Dahlgren	Y	F	7	Southwestern Cape SA; F.W.&S.K.Gess
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<i>A. linearis</i>	Y	M	1	Southwestern Cape SA; D.W.Gess
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<i>A. linearis</i>	Y		m	Southwestern Cape SA; F.W., S.K. & D.W.Gess
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<i>A. linearis</i>	Y	F	4	Western Escarpment SA; F.W.&S.K.Gess
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<i>A. linearis</i>	Y	M	2	Western Escarpment SA; F.W.&S.K.Gess
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<i>A. pulicifolia</i> Dahlgren	Y	F	24	Southwestern Cape SA; F.W.&S.K.Gess
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<i>A. pulicifolia</i>	Y	M	10	Southwestern Cape SA; F.W.&S.K.Gess
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<i>A. pulicifolia</i>	Y	M	3	Southwestern Cape SA; D.W.Gess
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<i>A. spinescens</i> Thunb.	Y	F	94	Southwestern Cape SA; F.W.&S.K.Gess
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<i>A. spinescens</i>	Y	M	13	Southwestern Cape SA; F.W.&S.K.Gess
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<i>A. spinescens</i>	Y	F	8	Southwestern Cape SA; D.W.Gess
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<i>A. spinescens</i>	Y	M	6	Southwestern Cape SA; D.W.Gess
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<i>A. spinescens</i>	Y	F	m	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. spinescens</i>	Y	M	m	Southwestern Cape SA; F.W.,S.K.&D.W.Gess
<i>A. vulnerans</i> Thunb.	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>A. sp./spp.</i>	Y	F	p	Southwestern Cape SA; S.K.Gess
<i>Lebeckia</i> Thunberg				
<i>L. sericea</i> Thunb.	Y	F	6	Namaqualand SA; F.W.&S.K.Gess
<i>L. sericea</i>	Y	M	3	Namaqualand SA; F.W.&S.K.Gess
<i>L. sericea</i>	Y	F	4	Namaqualand SA; D.W.Gess
<i>Masarina hyalinipennis</i> Richards				
Papilionaceae (Fabaceae)				
<i>Aspalathus</i> L.				
<i>A. spinescens</i> Thunb.	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>Lebeckia</i> Thunberg				
<i>L. sericea</i> Thunb.	Y	F	3	Namaqualand SA; M.Struck
<i>L. sericea</i>	Y	F	15	Namaqualand SA; F.W.&S.K.Gess
<i>L. sericea</i>	Y	M	1	Namaqualand SA; F.W.&S.K.Gess
<i>L. spinescens</i> Harv.	Y	F	1	Namaqualand SA; F.W.&S.K.Gess
<i>L. spinescens</i>	Y	M	3	Namaqualand SA; F.W.&S.K.Gess
<i>Wiborgia</i> Thunberg				
<i>W. monoptera</i> E. Mey.	YW	F	3	Namaqualand SA; F.W.&S.K.Gess
"papilionate"	YW	F	2	Namaqualand SA; T.F.Houston
<i>Masarina mixta</i> Richards				
Asteraceae (Compositae)				
<i>Athanasia</i> L.				
<i>A. trifurcata</i> L. (L.)	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess

## Campanulaceae

*Wahlenbergia* Schrad. ex Roth

<i>W. annularis</i> A. DC.	V	F	1	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. paniculata</i> (Thunb.) A.DC.	V	F	27	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. paniculata</i>	V	M	4	Southwestern Cape SA; D.W.Gess
<i>W. paniculata</i>	V	M	3	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. paniculata</i>	V	M	2	Southwestern Cape SA; D.W.Gess
<i>W. psammophila</i> Schltr.	PuV	F	3	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. psammophila</i>	PuV	M	4	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. sp.</i>	W	F	1	Southwestern Cape SA; S.K.Gess
<i>W. sp.</i>	V	F	4	Western Escarpment SA; F.W.&S.K.Gess

## Papilionaceae (Fabaceae)

*Aspalathus* L.

<i>A. spinescens</i> Thunb.	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess
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*Masarina strucki* Gess

## Sterculiaceae

*Hermannia* L.

<i>H. disermifolia</i> Jacq.	Y	F	1	Namaqualand SA; M.Struck
<i>H. disermifolia</i>	Y	F	12	Namaqualand SA; F.W.&S.K.Gess
<i>H. disermifolia</i>	Y	M	4	Namaqualand SA; F.W.&S.K.Gess
<i>H. disermifolia</i>	Y	F	3	Namaqualand SA; F.W.&S.K.Gess
<i>H. disermifolia</i>	Y	F	p	Namaqualand SA; S.K.Gess

*Masarina* sp. A

Papilionaceae (Fabaceae)

*Aspalathus* L.

<i>A. divaricata</i> Thunb.	Y	M	6	Southwestern Cape SA; S.K.Gess
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*Quartinia* Ed. André*Quartinia artemis* Richards

Asteraceae (Compositae)

*Leysera* L.

<i>L. tenella</i> DC.	Y	F	1	Western Escarpment SA; F.W.Gess
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*Quartinia atra* Schulthess

Aizoaceae: Mesembryanthema

"Mesembryanthemum"

–	–	–	South Africa; R.E.Turner in Turner 1939
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*Quartinia jocasta* Richards

Aizoaceae: non-Mesembryanthema

*Galenia* L.*G. filiformis* (Thunb.)

N.E.Br.	–	F	2	Namaqualand SA; M.Struck
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Asteraceae (Compositae)

*Leysera* L.

<i>L. gnaphalodes</i> (L.) L.	Y	F	1	Namaqualand SA; F.W.Gess
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*Quartinia media* Schulthess

Aizoaceae: Mesembryanthema

"Mesembryanthemum"

C	–	–	Southwestern Cape SA; R.E.Turner in Turner 1939
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*Quartinia ochraceopicta* Schulthess

Aizoaceae: Mesembryanthema

"mesem"

W	–	–	Southern Namibia; R.E. Turner in Turner 1939
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*Quartinia parcepunctata* Richards

## Campanulaceae

*Microcodon* A. DC.

<i>M. sparsiflorum</i> A.DC.	V	F	4	Southwestern Cape SA; F.W.&S.K.Gess
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*Wahlenbergia* Schrad. ex Roth

<i>W. cf. constricta</i> V. Brehmer	V	F	4	Southwestern Cape SA; F.W.&S.K.Gess
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<i>W. ecklonii</i> Buek	V	F	9	Southwestern Cape SA; F.W.,S.K.&H.W.Gess
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<i>W. paniculata</i> (Thunb.) A.DC.	V	F	13	Southwestern Cape SA; D.W.Gess
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<i>W. paniculata</i>	V	M	1	Southwestern Cape SA; D.W.Gess
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<i>W. paniculata</i>	V	F	8	Southwestern Cape SA; F.W.&S.K.Gess
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<i>W. paniculata</i>	V	M	1	Southwestern Cape SA; F.W.&S.K.Gess
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*Quartinia persephone* Richards

## Aizoaceae: Mesembryanthema

*Psilocalon* N.E.Br.*P. acutisepalum* (Berger)

N.E.Br.	WPi	F	1	Southwestern Cape SA; F.W.&S.K.Gess
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## Asteraceae (Compositae)

*Athanasia* L.

<i>A. trifurcata</i> (L.) L.	Y	F	1	Southwestern Cape SA; F.W.&S.K.Gess
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*Senecio* L.

S. sp.	Y	F	1	Western Escarpment SA; F.W.Gess
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## Campanulaceae

*Microcodon* A. DC.

<i>M. sparsiflorum</i> A.DC.	V	F	1	Southwestern Cape SA; D.W.Gess
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<i>M. sparsiflorum</i>	V	M	2	Southwestern Cape SA; D.W.Gess
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<i>M. sparsiflorum</i>	V	M	1	Southwestern Cape SA; F.W.&S.K.Gess
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<i>Wahlenbergia</i> Schrad. ex Roth				
<i>W. paniculata</i> (Thunb.) A.DC.	V	F	1	Southwestern Cape SA; D.W.Gess
<i>W. paniculata</i>	V	F	2	Southwestern Cape SA; S.K.Gess
<i>Quartinia punctulata</i> Schulthess				
Aizoaceae: Mesembryanthema				
<i>Mesembryanthemum</i> L.				
<i>M. crystallinum</i> L.	YW	—	—	Southern Namibia; R.E. Turner in Turner 1939
<i>M. crystallinum</i>	YW	—	—	Southern Great Karoo SA; R.E.Turner in Turner 1939
<i>M. crystallinum</i>	YW	—	—	Southwestern Cape SA; R.E.Turner in Turner 1939
<i>Quartinia vagepunctata</i> Schulthess				
Aizoaceae: Mesembryanthema				
“mesem”	—	—	—	Southern Africa; R.E. Turner in Turner 1939
Aizoaceae: non-Mesembryanthema				
<i>Galenia</i> L.				
<i>G. sp.</i>	Pi	F	1	Namaqualand SA; S.K.Gess
Asteraceae (Compositae)				
<i>Cotula</i> L.				
<i>C. leptalea</i> DC.	Y	F	1	Western Escarpment SA; F.W.&S.K.Gess
<i>C. leptalea</i> DC.	Y	M	6	Western Escarpment SA; F.W.&S.K.Gess
<i>C. sp.</i>	Y	F	2	Namaqualand SA; F.W.Gess
<i>C. sp.</i>	Y	F	7	Western Escarpment SA; F.W.&S.K.Gess
<i>C. sp.</i>	Y	M	1	Western Escarpment SA; F.W.&S.K.Gess
<i>cf. Helicbrysum</i>				
<i>cf. H. sp.</i>	Y	F	3	Namaqualand SA; S.K.Gess



<i>Leysera</i> L.				
<i>L. gnaphalodes</i> (L.) L.	Y	F	37	Namaqualand SA; F.W.&S.K.Gess
<i>L. gnaphalodes</i>	Y	M	6	Namaqualand SA; F.W.&S.K.Gess
<i>L. gnaphalodes</i>	Y	F	3	Western Escarpment SA; F.W.&S.K.Gess
<i>L. tenella</i> DC.	Y	F	59	Western Escarpment SA; F.W.,S.K.&D.W.Gess
<i>L. tenella</i>	Y	M	29	Western Escarpment SA; F.W.,S.K.&D.W.Gess
<i>L. tenella</i>	Y	F	m	Western Escarpment SA; F.W.,S.K.&D.W.Gess
<i>L. tenella</i>	Y	F	p	Western Escarpment SA; S.K.Gess
<i>Osteospermum</i> L.				
<i>O. cf. oppositifolia</i> (Ait.) T.Norl.	Y	M	1	Western Escarpment SA; D.W.Gess
<i>Pentzia</i> Thunb.				
<i>P. suffruticosa</i> (L.) Hutch. ex Merxm.	Y	F	2	Namaqualand SA; S.K.Gess
<i>P. suffruticosa</i>	Y	F	39	Western Escarpment SA; F.W.&S.K.Gess
<i>Relbania</i> L'Herit. emend. Bremer				
<i>R. sp.</i>	Y	F	19	Western Escarpment SA; F.W.&S.K.Gess
<i>R. sp.</i>	Y	M	5	Western Escarpment SA; F.W.&S.K.Gess
<i>Senecio</i> L.				
<i>S. sp. prob. nivea</i> Less.	W	F	5	Western Escarpment SA; F.W.Gess
<i>S. sp. prob. nivea</i>	W	M	5	Western Escarpment SA; F.W.Gess
Papilionaceae (Fabaceae)				
<i>Lebeckia</i> Thunb.				
<i>L. sericea</i> Thunb.	Y	M	1	Namaqualand SA; F.W.Gess

*Quartinia* sp. A

Aizoaceae: Mesembryanthema

*Leipoldtia* L. Bol.

<i>L. sp.</i>	Pi	F	1	Namaqualand SA; S.K.Gess
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*Polymita* N.E.Br.

<i>P. albiflora</i> (L.Bol.) L.Bol.	—	F	1	Namaqualand SA; M.Struck
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"mesem"	Pi	F	1	Western Escarpment SA; F.W.&S.K.Gess
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*Quartinia* sp. B

Aizoaceae: Mesembryanthema

*Prenia* N.E.Br.*P. sladeniana* (L.Bol.)

L.Bol.	—	F	1	Namaqualand SA; M.Struck
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*Quartinia* sp. D

Asteraceae (Compositae)

*Leysera* L.

<i>L. gnaphalodes</i> (L.) L.	Y	F	8	Namaqualand SA; F.W.&S.K.Gess
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<i>L. gnaphalodes</i>	Y	F	20	Western Escarpment SA; F.W.&S.K.Gess
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<i>L. gnaphalodes</i>	Y	M	5	Western Escarpment SA; F.W.&S.K.Gess
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<i>L. tenella</i> DC.	Y	F	4	Western Escarpment SA; S.K.Gess
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*Relbania* L'Herit. emend. Bremer

<i>R. sp.</i>	Y	F	2	Western Escarpment SA; F.W.&S.K.Gess
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*Senecio* L.

<i>S. prob. nivea</i> Less.	W	F	1	Western Escarpment SA; F.W.Gess
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*Quartinia* sp. E

Campanulaceae

*Lightfootia* l'Herit.

<i>L. namaquana</i> Sond.	Pi	F	21	Namaqualand SA; S.K.Gess
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*Wahlenbergia* Schrad. ex Roth

<i>W. pilosa</i> Buek	V	F	5	Namaqualand SA; S.K.Gess
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<i>W. pilosa</i>	V	M	2	Namaqualand SA; S.K.Gess
<i>Quartinia</i> sp. F				
Asteraceae (Compositae)				
<i>cf. Helichrysum</i> Mill.				
<i>cf. H. sp.</i>	Y	F	1	Namaqualand SA; D.W.Gess
Aizoaceae: Mesembryanthema				
<i>Leipoldtia</i> L. Bol.				
<i>L. sp.</i>	Pi	F	1	Namaqualand SA; D.W.Gess
<i>L. sp.</i>	Pi	M	5	Namaqualand SA; D.W.Gess
<i>Quartinia</i> sp. G				
Campanulaceae				
<i>Wahlenbergia</i> Schrad. ex Roth				
<i>W. pilosa</i> Buek	V	F	1	Namaqualand SA; S.K.Gess
<i>Quartinia</i> sp. H				
Campanulaceae				
<i>Wahlenbergia</i> Schrad. ex Roth				
<i>W. ecklonii</i> Buek	V	F	1	Southwestern Cape SA; S.K.Gess
<i>Quartinia</i> sp. I				
Asteraceae (Compositae)				
<i>Leysera</i> L.				
<i>L. gnaphaloides</i> (L.) L.	Y	F	7	Western Escarpment SA; F.W.&S.K.Gess
<i>L. gnaphaloides</i>	Y	M	1	Western Escarpment SA; F.W.&S.K.Gess

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### *Quartiniella* Schulthess

#### *Quartiniella watersoni* Schulthess

##### Asteraceae (Compositae)

###### *Athanasia* L.

<i>A. trifurcata</i> (L.) L.	Y	M	1	Tankwa Karoo SA; S.K.Gess
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<i>A. sp.</i>	Y	F	1	Tankwa Karoo SA; H.W.Gess
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<i>A. sp.</i>	Y	M	1	Tankwa Karoo SA; R.W.Gess
<i>Pentzia</i> Thunb.				
<i>P. suffruticosa</i> (L.) Hutch. ex Merxm.	Y	F	17	Tankwa Karoo SA; F.W.Gess
<i>P. suffruticosa</i>	Y	M	2	Tankwa Karoo SA; F.W.Gess
<i>P. suffruticosa</i>	Y	F	1	Tankwa Karoo SA; S.K.Gess

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### *Quartinioides* Richards

#### *Quartinioides antigone* Richards

##### Liliaceae

##### *Aloe* L.

<i>A. striata</i> Haw.	PiO	F	24	Southern Great Karoo SA; F.W.Gess
<i>A. striata</i>	PiO	M	5	Southern Great Karoo SA; F.W.Gess

#### *Quartinioides basuto* Richards

##### Asteraceae (Compositae)

##### *Aster* L.

<i>A. muricatus</i> Thunb.	BV	F	1	Lesotho; C.F.Jacot Guillarmod
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##### *Gazania* Gaertn.

<i>G. linearis</i> (Thunb.) Druce	Y	F	1	Lesotho; O.W.Richards in Richards 1962
<i>G. linearis</i>	Y	M	1	Lesotho; O.W.Richards in Richards 1962

#### *Quartinioides capensis* (Kohl)

##### Aizoaceae: Mesembryanthema

"Mesembryanthemum"	W	—	—	Southwestern Cape SA; R.E.Turner in Turner 1939
"Mesembryanthemum"	W	—	—	Southern Cape SA; R.E.Turner in Turner 1939

*Quartinioides cyllene* Richards

Asteraceae (Compositae)

*Athanasia* L.

<i>A. sp.</i>	Y	F	1	Tankwa Karoo SA; F.W.&S.K.Gess
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*Leysera* L.

<i>L. gnaphalodes</i> (L.) L.	Y	F	5	Namaqualand SA; F.W.&S.K.Gess
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<i>L. gnaphalodes</i>	Y	F	15	Western Escarpment SA; F.W.&S.K.Gess
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<i>L. gnaphalodes</i>	Y	M	6	Western Escarpment SA; F.W.&S.K.Gess
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*Relbania* L'Herit. emend Bremer

<i>R. pumila</i> Thunb.	Y	F	2	Western Escarpment SA; F.W.&S.K.Gess
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<i>R. pumila</i>	Y	M	1	Western Escarpment SA; F.W.&S.K.Gess
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*Senecio* L.

<i>S. sp. prob. nivea</i> Less.	W	F	3	Western Escarpment SA; F.W.Gess
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<i>S. sp. prob. nivea</i>	W	M	3	Western Escarpment SA; F.W.Gess
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*Quartinioides helichrysi* Richards

Asteraceae (Compositae)

*Helichrysum* Mill.

<i>H. fruticans</i> (L.) D.Don.	—	F	3	Lesotho; C.F.Jacot Guillarmod
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<i>H. fruticans</i> (L.) D.Don.	—	F	5	Lesotho; C.F.Jacot Guillarmod in Richards 1962
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*Quartinioides metallescens* (Schulthess)

Asteraceae (Compositae)

*Gazania* Gaertn.

<i>G. sp.</i>	—	F	1	Lesotho; C.F.Jacot Guillarmod
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<i>G. linearis</i> (Thunb.) Druce	Y	F	2	Lesotho; C.F.Jacot Guillarmod
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*Helichrysum* Mill.

<i>H. sp.</i>	—	F	1	Lesotho; C.F.Jacot Guillarmod in Richards 1962
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*Quartinioides niveopicta* (Schulthess)

Aizoaceae: Mesembryanthema

*"Mesembryanthemum"*

-	-	-	Southern Africa; R.E. Turner in Turner 1939
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Plumbaginaceae

*Limonium* Mill.*L. sp.*

V	F	1	Tankwa Karoo SA; S.K.Gess
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*Quartinioides poecila* (Schulthess)

Asteraceae (Compositae)

*Berkbeya* Ehrh.*B. sp.*

-	-	-	Namibia; R.E. Turner in Turner 1939
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*Quartinioides propinqua* (Schulthess)

Asteraceae (Compositae)

*Gazania* Gaertn.*G. sp.*

Y	F	1	Western Great Karoo SA; D.W.Gess
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*Quartinioides senecionis* Richards

Asteraceae (Compositae)

*Aster* L.*A. muricatus* Thunb.

BV	F	6	Lesotho; C.F.Jacot Guillarmod
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*A. muricatus*

BV	M	1	Lesotho; C.F.Jacot Guillarmod
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*A. muricatus*

BV	F	11	Lesotho; C.F.Jacot Guillarmod in Richards 1962
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*A. muricatus*

BV	M	7	Lesotho; C.F.Jacot Guillarmod in Richards 1962
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*Gazania* Gaertn.*G. sp.*

-	-	-	Lesotho; C.F.Jacot Guillarmod in Richards 1962
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*Senecio* L.*S. laevigatus* Thunb.

-	F	9	Orange Free State SA; C.F.Jacot Guillarmod
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*S. laevigatus*

-	M	1	Orange Free State SA; C.F.Jacot Guillarmod
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<i>S. laevigatus</i>	—	F	27	Orange Free State SA; C.F.Jacot Guillarmod in Richards 1962
<i>S. laevigatus</i>	—	M	2	Orange Free State SA; C.F.Jacot Guillarmod in Richards 1962
<i>Quartinioides signata</i> (Schulthess) Aizoaceae: Mesembryanthema "Mesembryanthemum"	—	—	—	Southern Africa; R.E. Turner in Turner 1939
<i>Quartinioides tarsata</i> Richards Aizoaceae: Mesembryanthema <i>Delosperma</i> N.E.Br. <i>D. acuminatum</i> L.Bol.	—	—	12	Eastern Cape SA; C.F.Jacot Guillarmod
<i>Drosanthemum</i> Schwant. <i>D. hispidum</i> (L.) Schwant.	Pi	F	2	Eastern Cape SA; E.McC.Callan
<i>D. hispidum</i>	Pi	F	1	Eastern Cape SA; E.McC.Callan in Richards 1962
Asteraceae (Compositae) <i>Berkheya</i> Ehrh. <i>B. fruticosa</i> (L.) Ehrh.	Y	F	1	Western Escarpment SA; D.W.Gess
<i>B. sp.</i>	Y	F	2	Western Great Karoo SA; F.W.&S.K.Gess
<i>B. sp.</i>	Y	M	1	Western Great Karoo SA; F.W.&S.K.Gess
<i>Gazania</i> Gaertn. <i>G. sp.</i>	Y	F	1	Western Great Karoo SA; F.W.&S.K.Gess
Scrophulariaceae <i>Aptosimum</i> Burch. <i>A. procumbens</i> (Lehm.)Steud.	BV	F	14	Eastern Cape SA; F.W.&S.K.Gess
<i>Peliostomum</i> Benth. <i>P. leucorrhizum</i> E. Mey. ex Benth. <i>P. leucorrhizum</i>	BV	F	12	Southern Kalahari SA; F.W.&S.K.Gess
	BV	M	1	Southern Kalahari SA; F.W.&S.K.Gess

<i>P. leucorrhizum</i>	BV	F	5	Northern Great Karoo SA; F.W.&S.K.Gess
<i>P. leucorrhizum</i>	BV	M	1	Northern Great Karoo SA; F.W.&S.K.Gess
<i>P. leucorrhizum</i>	BV	F	7	Western Great Karoo SA; F.W.,S.K.&D.W.Gess
<i>P. virgatum</i> E. Mey. ex Benth.	PV	F	3	Namaqualand SA; F.W.&S.K.Gess
<i>Quartinoides</i> sp. A				
Aizoaceae: Mesembryanthema				
<i>Drosanthemum</i> Schwant.				
<i>D. sp.</i>	Pi	F	1	Namaqualand SA; S.K. Gess
<i>Quartinoides</i> sp. B				
Aizoaceae: Mesembryanthema				
<i>Drosanthemum</i> Schwant.				
<i>D. sp.</i>	Pi	F	1	Namaqualand SA; S.K. Gess
<i>Quartinoides</i> sp. C				
Aizoaceae: Mesembryanthema				
<i>Drosanthemum</i> Schwant.				
<i>D. hispidum</i> (L.) Schwant.	Pi	F	1	Namaqualand SA; F.W.&S.K.Gess
<i>Quartinoides</i> sp. D				
Aizoaceae: Mesembryanthema				
<i>Drosanthemum</i> Schwant.				
<i>D. hispidum</i> (L.) Schwant.	Pi	F	1	Namaqualand SA; F.W.&S.K.Gess
<i>Psilocaulon</i> N.E.Br.				
<i>P. acutisepalum</i> (Berger) N.E.Br.	WPi	–	1	Namaqualand SA; F.W.&S.K.Gess
<i>Quartinoides</i> sp. E				
Aizoaceae: Mesembryanthema				
<i>Drosanthemum</i> Schwant.				
<i>D. hispidum</i> (L.) Schwant.	Pi	F	2	Namaqualand SA; F.W.&S.K.Gess
<i>D. hispidum</i>	Pi	M	1	Namaqualand SA; F.W.&S.K.Gess

*Quartinioides* sp. F

Aizoaceae: Mesembryanthema

*Psilocaulon* N.E.Br.*P. cf. articulatum* (Th.)

Schwant.

Pi

F

19

Southern Great Karoo SA;  
F.W.,S.K.&R.W.Gess*Sphalmanthus* N.E.Br.*S. cf. bijliae* (N.E.Br.)

L.Bol.

WPi

F

209

Southern Great Karoo SA;  
F.W.,S.K.&R.W.Gess*S. cf. bijliae*

WPi

M

8

Southern Great Karoo SA;  
F.W.,S.K.&R.W.Gess*Quartinioides* sp. G

Asteraceae (Compositae)

*Berkbeya* Ehrh.*B. cf. spinosa* (L.f.) Druce

Y

F

1

Southern Great Karoo SA;  
S.K.Gess*Quartinioides* sp. H

Aizoaceae: Mesembryanthema

*Drosanthemum* Schwant.*D. sp.*

Pi

F

17

West Coast SA;  
F.W.,S.K.&D.W.Gess*Quartinioides* sp. I

Aizoaceae: Mesembryanthema

*Drosanthemum* Schwant.*D. sp.*

Pi

F

3

Namaqualand SA;  
F.W.&S.K.Gess*Prenia* N.E.Br.*P. pallens* (Ait.) N.E.Br.

—

F

3

Namaqualand SA;  
M.Struck

"mesem"

Pi

F

1

Namaqualand SA;  
F.W.Gess

Asteraceae (Compositae)

*Arctotheca* Wendl.*A. calendula* (L.) Levyns

Y

F

2

Namaqualand SA;  
D.W.Gess

"daisy"

Y

F

4

Namaqualand SA;  
F.W.&S.K.Gess

*Quartinioides* sp. J

Aizoaceae: Mesembryanthema

"mesem"	Y	F	36	Little Karoo SA; F.W.&S.K.Gess
"mesem"	Y	M	1	Little Karoo SA; F.W.Gess
"mesem"	W	F	2	Western Escarpment SA; F.W.&S.K.Gess
"mesem"	W	M	2	Western Escarpment SA; F.W.&S.K.Gess

Plumbaginaceae

*Limonium* Mill.

<i>L. sp.</i>	V	F	5	Southwestern Karoo SA; F.W.&S.K.Gess
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*Quartinioides* sp. K

Aizoaceae: Mesembryanthema

"mesem"	YW	F	1	Eastern Cape SA; C.F.Jacot Guillarmod
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*Quartinioides* sp. M

Campanulaceae

*Wahlenbergia* Schrad. ex Roth

<i>W. pilosa</i> Buek	V	F	1	Namaqualand SA; S.K.Gess
<i>W. pilosa</i>	V	F	3	Namaqualand SA; S.K.Gess
<i>W. prostrata</i> A.DC.	V	F	16	Namaqualand SA; F.W.,S.K.&D.W.Gess
<i>W. prostrata</i>	V	M	2	Namaqualand SA; S.K.Gess

*Quartinioides* sp. N

Campanulaceae

*Wahlenbergia* Schrad. ex Roth

<i>W. paniculata</i> (Thunb.) A.DC.	V	F	6	Southwestern Cape SA; F.W.&S.K.Gess
<i>W. sp.</i>	V	F	16	Western Escarpment SA; F.W.&S.K.Gess
<i>W. sp.</i>	V	M	3	Western Escarpment SA; F.W.&S.K.Gess



*Quartinioides* sp. O

Aizoaceae: Mesembryanthema

*Polymita* N. E. Br.

<i>P. albiflora</i> (L. Bol.) L. Bol.	–	F	1	Namaqualand SA; M. Struck
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*Prenia* N. E. Br.

<i>P. pallens</i> (Ait.) N. E. Br.	–	F	1	Namaqualand SA; M. Struck
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*Stoeberia* Dinter & Schwant.

<i>S. sp.</i>	Pi	F	6	Bushmanland SA; F.W., S.K. & D.W. Gess
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*Quartinioides* sp. P

Aizoaceae: Mesembryanthema

*Prenia* N. E. Br.

<i>P. pallens</i> (Ait.) N. E. Br.	–	F	4	Namaqualand SA; M. Struck
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<i>P. sladeniana</i> (L. Bol.) L. Bol.	–	F	1	Namaqualand SA; M. Struck
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*Quartinioides* sp. Q

Aizoaceae: Mesembryanthema

*Stoeberia* Dinter & Schwant.

<i>S. sp.</i>	Pi	M	1	Bushmanland SA; D.W. Gess
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*Quartinioides* sp. R

Aizoaceae: Mesembryanthema

*Stoeberia* Dinter & Schwant.

<i>S. sp.</i>	Pi	M	1	Bushmanland SA; D.W. Gess
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*Quartinioides* sp. S

Campanulaceae

*Wahlenbergia* Schrad. ex Roth

<i>W. paniculata</i> (Thunb.) A. DC.	V	M	1	Southwestern Cape SA; D.W. Gess
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*Quartinioides* sp. T

Aizoaceae: Mesembryanthema

*Drosanthemum* Schwant.

<i>D. sp.</i>	Pi	F	5	Namaqualand SA; F.W. & S.K. Gess
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<i>D. sp.</i>	Pi	M	1	Namaqualand SA; S.K. Gess
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Scrophulariaceae					
<i>Peliostomum</i> Benth.					
<i>P. virgatum</i> E.Mey.	PuV	F	2	Namaqualand SA; S.K.Gess	
<i>Quartinioides</i> sp. U					
Campanulaceae					
<i>Wahlenbergia</i> Schrad. ex Roth					
<i>W. ecklonii</i> Buek	V	F	5	Southwestern Cape SA; S.K.&H.W.Gess	
<i>W. ecklonii</i>	V	M	1	Southwestern Cape SA; F.W.Gess	
<i>Quartinioides</i> sp. V					
Scrophulariaceae					
<i>Peliostomum</i> Benth.					
<i>P. leucorrhizum</i> E. Mey. ex Benth.	BV	F	3	Southern Kalahari SA; F.W.&S.K.Gess	
<i>Quartinioides</i> sp. W					
Scrophulariaceae					
<i>Peliostomum</i> Benth.					
<i>P. leucorrhizum</i> E. Mey. ex Benth.	BV	F	1	Southern Kalahari SA; F.W.&S.K.Gess	
<i>Quartinioides</i> sp. X					
Scrophulariaceae					
<i>Peliostomum</i> Benth.					
<i>P. leucorrhizum</i> E. Mey. ex Benth.	BV	F	1	Southern Kalahari SA; F.W.&S.K.Gess	
<i>Quartinioides</i> sp. Y					
Aizoaceae: Mesembryanthema					
<i>Drosanthemum</i> Schwant.					
<i>D. sp.</i>	Pi	F	5	Namaqualand SA; S.K.Gess	
Scrophulariaceae					
<i>Peliostomum</i> Benth.					
<i>P. virgatum</i> E.Mey.	PuV	M	1	Namaqualand SA; S.K.Gess	
<i>Quartinioides</i> sp. Z					
Asteraceae (Compositae)					
<i>Gazania</i> Gaertn.					
<i>G. sp.</i>	Y	F	2	Western Karoo SA; F.W.,S.K.&D.W.Gess	

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 AUSTRALIAN REGION
 

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*Ammoparagia* Snelling*Ammoparagia bua* Snelling

## Goodeniaceae

*Goodenia* Sm.*G. berardiana* Gaudich.

Y

F

2

Western Aus; Howard &  
Houston in Snelling  
1986*G. berardiana*

Y

M

1

Western Aus; Howard &  
Houston in Snelling  
1986*G. berardiana*

Y

M

1

Western Aus; Houston &  
Hanich in Snelling 1986

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*Paragia* Shuckard
*Paragia decipiens* Shuckard

## Myrtaceae

*Eucalyptus* L'Herit.*E. camaldulensis* Dehnh.

—

F

m

New South Wales Aus;  
Naumann & Cardale  
1987*E. camaldulensis*

—

F

p

New South Wales Aus;  
Naumann & Cardale  
1987*Paragia monocesta* Snelling

## Myrtaceae

*Calythrix* Labill.*C. oldfieldii* Benth.

—

F

10

Western Aus; Howard &  
Houston in Snelling  
1986*Verticordia* DC.*V. forrestii* F.Muell.

—

F

1

Western Aus; Howard &  
Houston in Snelling  
1986

*Paragia nasuta* F.Smith

## Myrtaceae

*Melaleuca* L.

<i>M. fulgens</i> R.Br.	—	F	5	Western Aus; Houston in Snelling 1986
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<i>M. fulgens</i>	—	M	4	Western Aus; Houston in Snelling 1986
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<i>M. cf. steedmanii</i> C.A.Gardn.	C	F	3	Western Aus; F.W.,S.K.& R.W.Gess
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<i>M. cf. steedmanii</i>	C	M	1	Western Aus; F.W.,S.K.& R.W.Gess
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<i>M. glaberrima</i> F.Muell.	PuPi	F	1	Western Aus; F.W.,S.K.& R.W.Gess
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<i>M. glaberrima</i>	PuPi	M	3	Western Aus; F.W.,S.K.& R.W.Gess
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## Proteaceae

*Grevillea* R.Br.

<i>G. paradoxa</i> F.Muell.	PiR	M	1	Western Aus; Houston in Snelling 1986
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<i>G. sp.</i>	WY	F	3	Western Aus; F.W.,S.K.& R.W.Gess
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<i>G. sp.</i>	WY	M	5	Western Aus; F.W.,S.K.& R.W.Gess
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*Paragia oligomera* Snelling

## Bromeliaceae

*Regelia* Schau.

<i>R. ciliata</i> Schau.	—	F	1	Western Aus; Houston in Snelling 1986
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*Paragia sobrina* F.Smith

## Myrtaceae

*Beaufortia* R.Br.

<i>B. bracteosa</i> Diels	—	F	2	Western Aus; Houston in Snelling 1986
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*Paragia tricolor* Smith

## Myrtaceae

*Eucalyptus* L'Herit.

<i>E. calophylla</i> R.Br.	—	F	10p	Southwestern Aus; Houston 1984
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<i>E. cylindriflora</i> Maiden & Blakely	W	F	m	Southwestern Aus; Houston 1984
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*Paragia vespiformis* Smith

## Mimosaceae

*Acacia* (Tourn.) L.

<i>A. blakelyi</i> Maiden	—	F	p	Western Aus; Houston 1986
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## Myrtaceae

*Eucalyptus* L'Herit.

<i>E. oldfieldii</i> F. Muell.	—	—	—	Western Aus; Houston 1986
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*Melaleuca* L.

<i>M. nematophylla</i> F. Muell.	Pi	—	—	Western Aus; Houston 1986
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*M. scabra* R.Br.

Pi	—	—	Western Aus; Houston 1986
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*M. uncinata* R.Br.

—	—	—	Western Aus; Houston 1986
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*Scholtzia* Schau.

<i>S. drummondii</i> Benth.	—	—	—	Western Aus; Houston 1986
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## Proteaceae

*Grevillea* R.Br.

<i>G. teretifolia</i> Meissn.	W	—	—	Western Aus; Houston 1986
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*Riekia* Richards*Riekia confluens* (Snelling)

## Goodeniaceae

*Goodenia* Sm.

<i>G. berardiana</i> Gaudich.	Y	F	1	Western Aus; Howard & Houston in Snelling 1986
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*G. berardiana*

Y	M	1	Western Aus; Houston & Hanich in Snelling 1986
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*Lechenaultia* R.Br.

<i>L. sp.</i>	Y	F	44	Western Aus; F.W., S.K. & R.W. Gess
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<i>L. sp.</i>	Y	M	4	Western Aus; F.W., S.K. & R.W. Gess
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*Riekia nocatunga* Richards

## Goodeniaceae

*Goodenia* R.Br.

<i>G. cycloptera</i> R.Br.	Y	F	5	New South Wales Aus; Richards 1968
<i>G. fascicularis</i> F.Muell. & Tate	Y	F	11	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. fascicularis</i>	Y	M	1	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. pinnatifida</i> Schldl.	Y	F	8	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. pinnatifida</i>	Y	M	1	Queensland Aus; F.W., S.K.&R.W.Gess

*Rolandia* Richards*Rolandia angulata* (Richards)

## Goodeniaceae

*Goodenia* R.Br.

<i>G. cycloptera</i> R.Br.	Y	F	12	Queensland Aus; Richards 1968
<i>G. cycloptera</i>	Y	F	37	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. cycloptera</i>	Y	M	10	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. pinnatifida</i> Schldl.	Y	F	57	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. pinnatifida</i>	Y	M	31	Queensland Aus; F.W., S.K.&R.W.Gess
<i>G. sp.</i>	Y	F	6p	Queensland Aus; S.K.Gess

*Rolandia borriveriae* Snelling

## Rubiaceae

*Borreria* G.F.W.Mey.

<i>B. exserta</i> K.Schum.	—	F	4	Northern Territory Aus; Cardale in Snelling 1986
<i>B. exserta</i>	—	M	3	Northern Territory Aus; Cardale in Snelling 1986

*Rolandia houstoni* Snelling

## Goodeniaceae

*Goodenia* R.Br.*G. berardiana* Gaudich.

Y

F

6

Western Aus; Howard and  
Houston in Snelling  
1986*G. berardiana*

Y

M

5

Western Aus; Howard and  
Houston in Snelling  
1986

## Myrtaceae

*Pileanthus* Labill.*P. peduncularis* Endl.

O

M

1

Western Aus; Howard and  
Houston in Snelling  
1986

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## APPENDIX 2 *Plants of the groups associated with masarine wasps in southern Africa together with their non-masarine solitary aculeate wasp and bee visitors*

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This list is derived from a survey of flower visiting by aculeate wasps and bees in the semi-arid areas of southern Africa (Gess 1992b). The survey took in 35 families of flowering plants, which were being visited in total by 616++ species of aculeate wasps and bees.

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### AIZOACEAE

The Aizoaceae are here presented in two groups, the non-Mesembryanthema and the Mesembryanthema. The Mesembryanthema are divided into flower form categories, those represented in the list being: stamen carpet flowers; central cone flowers; and cup flowers (adapted from Vogel 1954 and Hartmann 1991 and amended in the present study). Those "mesems" for which insufficient information was available for categorization are listed separately at the end.

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### AIZOACEAE—NON-MESEMBRYANTHEMA

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*Coelanthum* E. Mey.

*Coelanthum grandiflorum* E.Mey. ex Fenzl

Clanwilliam/  
Graafwater

Vespidae: Masarina

*Celonites bergenwahliae* Gess

*Celonites latitarsis* Gess

*Celonites wahlenbergiae* Gess

Nyssonidae

*Bembecinus* sp. A

*Bembecinus* sp. B

Anthophoridae

*Pseudodichroa capensis* (Friese)

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*Galenia* L.*Galenia africana* L.

Nieuwoudtville

Megachilidae

*Hoplitis* sp. L*Galenia filiformis* (Thunb.) N.E.Br.

Springbok

Vespidæ: Masarinae

*Quartinia jocasta* Richards*Galenia*. sp.

Anenous

Vespidæ: Masarinae

*Quartinia vagepunctata*  
Schulthess

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*Limeum* L.*Limeum* sp.

Nossob

Andrenidae

*Meliturgula* sp. A

Megachilidae

*Oranthebidium folliculosum*  
(Buysson)*Limeum aethiopicum* Burm.

Twee Rivieren

Larridae

*Tachysphex* Kalahari sp. A

Nyssonidae

*Bembecinus* Kalahari sp. A*Bembix zinni* Gess

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AIZOACEAE—MESEMBRYANTHEMA

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Stamen carpet flowers

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*Aridaria* N.E.Br.*Aridaria dyeri* L.Bol.

Alicedale

Vespidæ: Masarinae

*Ceramius linearis* Klug*Aridaria plenifolia* (N.E.Br.) Stearn

Alicedale

Vespidæ: Masarinae

*Ceramius capicola* Brauns*Ceramius linearis* Klug*Aridaria* sp.

Clanwilliam/Klawer

Vespidæ: Masarinae

*Ceramius cerceriformis*  
Saussure

Grahamstown

Vespidæ: Masarinae

*Ceramius lichtensteinii* (Klug)  
*Ceramius linearis* Klug

*Carpobrotus* N.E.Br.*Carpobrotus* sp.

Paleisheuvel

Scoliidae

Halictidae

*Cathimeris capensis* (Saussure)*Lasioglossum* sp. A*Drosanthemum* Schwant.*Drosanthemum floribundum* (Haw.) Schwant.

Grahamstown

Vespidae: Masarinae

*Ceramius linearis* Klug*Ceramius capicola* Brauns*Drosanthemum hispidum* (L.) Schwant.

Grahamstown

Vespidae: Masarinae

*Quartinioides tarsata* Richards

Halictidae

*Nomioides* sp.

Springbok

Vespidae: Masarinae

*Quartinioides* sp. C*Quartinioides* sp. D*Quartinioides* sp. E*Drosanthemum parvifolium* (Haw.) Schwant.

Grahamstown

Vespidae: Masarinae

*Jugurtia confusa* Richards*Drosanthemum* sp. (flowers pink)

Nieuwoudtville

Chrysididae

*Allocoelia glabra* Edney

Vespidae: Masarinae

*Ceramius bicolor* (Thunberg)*Jugurtia braunsi* (Schulthess)*Drosanthemum* sp. (flowers purplish pink)

Grahamstown

Scoliidae

*Cathimeris capensis* (Saussure)*Drosanthemum* sp. (flowers pink)

Springbok

Vespidae: Masarinae

*Jugurtia braunsi* (Schulthess)*Drosanthemum* sp. (flowers pink)

Anenous

Vespidae: Masarinae

*Quartinioides* sp. I*Quartinioides* sp. T*Quartinioides* sp. Y*Drosanthemum* sp. (flowers pink)

Bitterfontein/Garies

Vespidae: Masarinae

*Quartinioides* sp. A*Quartinioides* sp. B*Drosanthemum* sp. (flowers pink)

Port Nolloth

Vespidae: Masarinae

*Quartinioides* sp. H



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*Malephora* N.E.Br.*Malephora* sp.

Grahamstown

Vespidæ: Masarinae

*Ceramius linearis* Klug

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*Mesembryanthemum* L.*Mesembryanthemum aitonis* Jacq.

Grahamstown

Vespidæ: Masarinae

*Ceramius capicola* Brauns*Ceramius linearis* Klug*Ceramius lichtensteinii* (Klug)*Mesembryanthemum crystallinum* L.

Aus

Vespidæ: Masarinae

*Quartinia punctulatum*

Schulthess

Matjesfontein

Vespidæ: Masarinae

*Quartinia punctulatum*

Schulthess

Prince Albert Road

Vespidæ: Masarinae

*Quartinia punctulatum*

Schulthess

Vioolsdrif

Melittidae

*Capicola braunsiana* Friese

Willowmore

Vespidæ: Masarinae

*Ceramius cerceriformis*

Saussure

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*Platythyra* N.E.Br.*Platythyra haeckeliana* (Berger) N.E.Br.

Colchester,

Port Elizabeth

Vespidæ: Masarinae

*Ceramius capicola* Brauns

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"Mesem" (flowers white)

Touws River

Tiphidae

*Meria* sp. H

Vespidæ: Eumeninae

*Delta emarginatum* (L.)

Colletidae

*Colletes* sp. D

Matroosberg

Chrysididae

*Stilbum cyanurum* (Förster)

Tiphidae

*Meria* sp. H

Vespidæ: Eumeninae

*Delta caffer* (L.)*Raphiglossa natalensis* Smith

Pompilidae

*Hemipepsis vindex* Smith

Montagu/Matroosberg	Nyssonidae	<i>Stizus dewitzii</i> Handlirsch
	Halictidae	<i>Halictus</i> sp. A cf. <i>jucundus</i> Smith
		<i>Halictus</i> ( <i>Seladonia</i> ) sp. B
		<i>Lasioglossum</i> sp. A
	Anthophoridae	<i>Amegilla niveata</i> (Fries)
		<i>Tetraloniella junodi</i> (Fries)
	Tiphiidae	<i>Anthobosca erythrosoma</i> (Cameron)
		<i>Meria</i> sp. H
	Scoliidae	<i>Cathimeris capensis</i> (Saussure)
		<i>Scolia chrystotricha</i> Burmeister
Bloutoring	Sphecidae	<i>Podalonia canescens</i> (Dahlbom)
	Philanthidae	<i>Philanthus triangulum</i> (Fabricius)
	Megachilidae	<i>Megachile stellarum</i> Cockerell
	Anthophoridae	<i>Amegilla niveata</i> (Fries)
		<i>Amegilla spilostoma</i> (Cameron)
		<i>Xylocopa io</i> Vachal
	Sphecidae	<i>Spheg decipiens</i> Kohl
	Anthophoridae	<i>Xylocopa lugubris</i> Gerstaecker

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### Central cone flowers

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#### *Leipoldtia* L.Bol.

<i>Leipoldtia</i> sp. Springbok	Vespidae: Masarinae	<i>Jugurtia braunsi</i> (Schulthess)
		<i>Quartinia</i> sp. A
		<i>Quartinia</i> sp. F
	Megachilidae	<i>Hoplitis</i> sp. M

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#### *Mestoklema* N.E.Br.

#### *Mestoklema tuberosum* (L.) N.E.Br.

Grahamstown	Vespidae: Masarinae	<i>Ceramius capicola</i> Brauns
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*Polymita* N.E.Br.*Polymita albiflora* (L.Bol.) L.Bol.

Springbok

Vespidae: Masarinae

*Quartinia* sp. A*Quartinioides* sp. O

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*Prenia* N.E.Br.*Prenia sladeniana* (L.Bol.)

Springbok

Vespidae: Masarinae

*Quartinia* sp. B*Quartinioides* sp. P*Prenia pallens* (Ait.) N.E.Br.

Springbok

Vespidae: Masarinae

*Quartinioides* sp. I*Quartinioides* sp. O*Quartinioides* sp. P

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*Psilocaulon* N.E.Br.*Psilocaulon acutisepalum* (Berger) N.E.Br.

Springbok

Vespidae: Masarinae

*Ceramius bicolor* (Thunberg)*Ceramius cerceriformis*

Saussure

*Jugurtia calcarata* Richards*Quartinioides* sp. D

Clanwilliam

Vespidae: Masarinae

*Ceramius socius* Turner

Megachilidae

*Hoplitis* sp. K

Clanwilliam/Klawer

Vespidae: Masarinae

*Ceramius cerceriformis*

Saussure

*Quartinia persephone* Richards*Heriades* sp. A

Clanwilliam/Graafwater

Vespidae: Masarinae

*Ceramius peringueyi* Brauns

Klawer

Vespidae: Masarinae

*Ceramius bicolor* (Thunberg)

Vredendal

Vespidae: Masarinae

*Ceramius peringueyi* Brauns*Psilocaulon cf. articulatum* (Th.) Schwant.

Prince Albert

Vespidae: Masarinae

*Quartinioides* sp. F*Psilocaulon cf. subnodosum* (Berger) N.E.Br.

Graafwater

Vespidae: Masarinae

*Ceramius peringueyi* Brauns

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*Ruschia* Schwant.*Ruschia* sp. (flowers white)

Grahamstown	Vespidae: Masarinae	<i>Ceramius capicola</i> Brauns <i>Ceramius lichtensteinii</i> (Klug) <i>Ceramius linearis</i> Klug
	Vespidae: Eumeninae	<i>Delta caffer</i> (L.)
	Pompilidae	<i>Cyphononyx flavicornis</i> Fabricius <i>Hemipepsis brunniceps</i> Taschenberg

*Ruschia* sp. (flowers white)

Vioolsdrif	Anthophoridae	<i>Xylocopa caffra</i> (L.) <i>Xylocopa scioensis</i> Gribodo
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*Ruschia* sp. (flowers purplish pink)

Alicedale	Vespidae: Masarinae	<i>Ceramius lichtensteinii</i> (Klug) <i>Ceramius linearis</i> Klug
Grahamstown	Vespidae: Eumeninae	<i>Alastor</i> sp. 4

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*Sphalmanthus* N.E.Br.*Sphalmanthus* cf. *bijliae* (N.E.Br.) L.Bol.

43 km ENE Ceres	Vespidae: Masarinae	<i>Ceramius bicolor</i> (Thunberg)
	Halictidae	<i>Halictus</i> ( <i>Seladonia</i> ) sp. B
Prince Albert	Vespidae: Masarinae	<i>Ceramius beyeri</i> Brauns <i>Ceramius lichtensteinii</i> (Klug) <i>Quartinioides</i> sp. F
	Megachilidae	<i>Heriades</i> sp. I

*Sphalmanthus* sp.

Clanwilliam/Klawer	Vespidae: Eumeninae	<i>Delta caffer</i> (L.)
Nieuwoudtville	Vespidae: Masarinae	<i>Ceramius bicolor</i> (Thunberg)

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*Stoeberia* Dinter & Schwant.*Stoeberia* sp.

Aggeneys	Chrysididae	<i>Allocoelia mocsaryi</i> (Brauns)
	Vespidae: Masarinae	<i>Quartinioides</i> sp. O <i>Quartinioides</i> sp. Q <i>Quartinioides</i> sp. R

## white cone flowers

Nieuwoudtville

Vespididae: Masarinae

*Jugurtia braunsi* (Schulthess)*Jugurtia duplicata* Richards

## Cup flowers

*Herrea* Schwant.*Herrea* sp. A

Nieuwoudtville

Vespididae: Masarinae

*Jugurtia braunsi* (Schulthess)

Colletidae

*Scrapper* sp. A*Scrapper* sp. I

Halictidae

*Lasioglossum* sp. A*Lasioglossum* sp. D*Patellapsis* sp. A*Zonalictus* sp. D

Melittidae

*Melitta* sp. A

Megachilidae

*Nigranthidium concolor*  
(Friese)*Spinanthidium volkmanni*  
(Friese)

Anthophoridae

*Ceratina* sp. L*Herrea* sp. B

Clanwilliam/Citrusdal

Halictidae

*Lasioglossum* sp. A

Clanwilliam/Graafwater

Scoliidae

*Cathimeris capensis* (Saussure)

Vespididae: Masarinae

*Celonites bergenwahliae* Gess*Celonites wahlenbergiae* Gess

Colletidae

*Colletes* sp. E*Scrapper* sp. A

Halictidae

*Lasioglossum* sp. A*Lasioglossum* sp. D

Anthophoridae

*Sphecodopsis* sp.

Paleisheuwel

Colletidae

*Scrapper* sp. A*Scrapper* sp. B



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 "Mesems" not specified
 

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Anenous	Vespidae: Masarinae	<i>Quartinioides</i> sp. I
Aus	Vespidae: Masarinae	<i>Quartinia ochraceopicta</i> Schulthess
43 km ENE Ceres	Nyssonidae	<i>Bembecinus rhopaloceroides</i> (Arnold)
Clanwilliam/Klawer	Philanthidae	<i>Philanthus rugosus</i> Kohl
Die Koo	Halictidae	<i>Zonalictus</i> sp. C
Elim	Philanthidae	<i>Cerceris</i> sp. A
Garies	Vespidae: Masarinae	<i>Ceramius cerceriformis</i> Saussure
Grahamstown	Vespidae: Eumeninae	<i>Alastor</i> sp. 1 <i>Delta caffer</i> (L.) <i>Euodynerus</i> sp. <i>Katamenes macrocephalus</i> (Saussure) <i>Parachilus capensis</i> (Saussure)
	Vespidae: Masarinae	<i>Ceramius beyeri</i> Brauns <i>Ceramius capicola</i> Brauns <i>Ceramius lichtensteinii</i> (Klug) <i>Ceramius linearis</i> Klug
	Pompilidae	<i>Hemipepsis brunniceps</i> Taschenberg
	Sphecidae	<i>Isodontia simoni</i> (du Buysson) <i>Sphex decipiens</i> Kohl
	Nyssonidae	<i>Stizus dewitzii</i> Handlirsch
	Andrenidae	<i>Meliturgula braunsi</i> Friese
	Anthophoridae	<i>Ceratina</i> sp. F <i>Xylocopa lugubris</i> Gerstaecker <i>Xylocopa sicheli</i> Vachal
Hofmeyr	Vespidae: Masarinae	<i>Ceramius capicola</i> Brauns
Kommadagga	Vespidae: Masarinae	<i>Ceramius lichtensteinii</i> (Klug) <i>Ceramius linearis</i> Klug
	Anthophoridae	<i>Amegilla punctifrons</i> (Walker)
Montagu/Touws River	Vespidae: Masarinae	<i>Ceramius socius</i> Turner
Mossel Bay	Vespidae: Masarinae	<i>Quartinioides capensis</i> (Schulthess)

Nieuwoudtville	Vespididae: Masarinae	<i>Jugurtia braunsi</i> (Schulthess)
		<i>Quartinia</i> sp. A
		<i>Quartinoides</i> sp. J
	Melittidae	<i>Capicola braunsiana</i> Friese
	Megachilidae	<i>Hoplitis</i> sp. K
	Anthophoridae	<i>Ceratina</i> sp. G
Oudtshoorn	Vespididae: Masarinae	<i>Quartinoides</i> sp. J
	Philanthidae	<i>Cerceris curvitaris</i> Schletterer
	Halictidae	<i>Halictus (Seladonia)</i> sp. B
Springbok	Vespididae: Masarinae	<i>Jugurtia braunsi</i> (Schulthess)
Touws River	Colletidae	<i>Colletes</i> sp. D
	Halictidae	<i>Lasioglossum</i> sp. A
Vredendal	Sphecidae	<i>Podalonia canescens</i> (Dahlbom)
Worcester	Vespididae: Masarinae	<i>Quartinia media</i> Schulthess
Willowmore	Vespididae: Masarinae	<i>Quartinoides</i> sp. K
?	Vespididae: Masarinae	<i>Quartinoides niveopicta</i> (Schulthess)
?	Vespididae: Masarinae	<i>Quartinoides signata</i> (Schulthess)

## ASTERACEAE

The Asteraceae (Compositae) are here presented grouped in tribes following Hilliard (1977).

### Tribe 1 : Vernonieae

Flowers purple, violet, or white, rarely yellowish; tropical and subtropical.

### Tribe 2 : Eupatorieae

Corolla purplish, rose, or white, never distinctly yellow; mostly American.

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Tribe 3 : Astereae

Disc flowers usually yellow, yellowish, or white; ray flowers variously colored; worldwide, mostly in temperate and montane areas.

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*Chrysocoma* L.

*Chrysocoma ciliata* L.

Grahamstown

Sphecidae

*Ammophila bonaespei*

Lepelletier

Nyssonidae

*Bembix sibilans* Handlirsch

Anthophoridae

*Ceratina* sp. F
*Chrysocoma* sp.

Nieuwoudtville

Colletidae

*Scapter* sp. G

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*Conyza* Less.

*Conyza bonariensis* (L.) Cronq.

Grahamstown

Sphecidae

*Ammophila conifera* Arnold*Podalonia canescens* (Dahlbom)

Larriidae

*Tachysphex* sp. A

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*Felicia* Cass.

*Felicia* sp.

Springbok

Vespidae: Masarinae

*Jugurtia braunsiella*

(Schulthess)

## “blue rayed”

Die Bos

Vespidae: Masarinae

*Ceramius toriger* Schulthess

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*Pteronia* L.

*Pteronia divaricata* (including *P. cf. divaricata*) (Berg.) Less.

Clanwilliam

Vespidae: Masarinae

*Jugurtia braunsi* (Schulthess)

Nieuwoudtville

Tiphidae

*Mesa* sp. C

Vespidae: Masarinae

*Celonites promontorii* Brauns*Ceramius toriger* Schulthess*Jugurtia braunsi* (Schulthess)

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		<i>Jugurtia braunsiella</i> (Schulthess)
		<i>Jugurtia duplicata</i> Richards
	Nyssonidae	<i>Bembix cameronis</i> Handlirsch
	Megachilidae	<i>Heriades</i> sp. C
		<i>Heriades</i> sp. E
		<i>Hoplitis</i> sp. B
		<i>Hoplitis</i> sp. L
	Anthophoridae	<i>Nomada gigas</i> Friese
<i>Pteronia incana</i> (Burm.) DC.		
Barrydale	Vespidae: Masarinae	<i>Ceramius jacoti</i> Richards
<i>Pteronia paniculata</i> Thunb.		
Grahamstown	Vespidae: Masarinae	<i>Jugurtia braunsiella</i> (Schulthess)
<i>Pteronia</i> sp. B		
Springbok	Sphecidae	<i>Ammophila punctaticeps</i> (Arnold)
		<i>Podalonia canescens</i> (Dahlbom)
	Megachilidae	<i>Carinanthidium cariniventre</i> (Friese)
	Anthophoridae	<i>Anthophora wartmanni</i> Friese
		<i>Tetraloniella</i> sp.
<i>Pteronia</i> sp.		
Nieuwoudtville	Anthophoridae	<i>Anthophora</i> sp.
<i>Pteronia</i> sp.		
Springbok	Vespidae: Masarinae	<i>Ceramius rex</i> Saussure
		<i>Jugurtia braunsiella</i> (Schulthess)

#### Tribe 4 : Inuleae

Flowers usually yellow, occasionally whitish or red; worldwide.

#### *Helichrysum* Mill.

*Helichrysum ericaefolium* Less.

Grahamstown

Nyssonidae

*Bembecinus cinguliger* (Smith)

*Helichrysum cf. hebelepis* DC. (including *Helichrysum* sp.)

Clanwilliam/ Graafwater	Chrysididae	<i>Hedychrum coelestinum</i> Spinola
	Tiphiidae	<i>Meria</i> sp. H
	Vespidae: Masarinae	<i>Celonites wahlenbergiae</i> Gess
	Nyssonidae	<i>Bembecinus mutabilis</i> (Arnold) <i>Bembecinus</i> sp. A <i>Bembecinus</i> sp. B
	Crabronidae	<i>Belomicrus</i> sp. F
	Philanthidae	<i>Cerceris languida languida</i> Cameron
	Colletidae	<i>Scrapter</i> sp. F <i>Scrapter</i> sp. O
	Anthophoridae	<i>Sphecodopsis</i> sp.
<i>Helichrysum</i> sp. Bains Kloof	Philanthidae	<i>Philanthus histrio</i> Fabricius
<i>Helichrysum</i> sp. Clanwilliam	Megachilidae	<i>Heriades</i> sp. H
<i>Helichrysum</i> sp. Clanwilliam/Citrusdal	Megachilidae	<i>Heriades</i> sp. A
<i>Helichrysum</i> sp. Anenous	Vespidae: Masarinae	<i>Quartinia vagepunctata</i> Schulthess
Springbok	Vespidae: Masarinae	<i>Quartinia</i> sp. F

*Leysera* L.*Leysera gnaphalodes* (L.) L.

Anenous	Vespidae: Masarinae	<i>Quartinia vagepunctata</i> Schulthess <i>Quartinioides cyllene</i> Richards
Nieuwoudtville	Vespidae: Eumeninae	<i>Raphiglossa flavo-ornata</i> Cameron
	Vespidae: Masarinae	<i>Jugurtia polita</i> Richards <i>Jugurtia</i> sp. C <i>Quartinia vagepunctata</i> Schulthess <i>Quartinia</i> sp. I <i>Quartinia</i> sp. D



Springbok	Megachilidae	<i>Heriades</i> sp. F <i>Hoplitis</i> sp. L
	Vespidae: Eumeninae	<i>Raphiglossa flavo-ornata</i> Cameron
	Vespidae: Masarinae	<i>Jugurtia braunsi</i> (Schulthess) <i>Quartinia jocasta</i> Richards <i>Quartinia vagepunctata</i> Schulthess <i>Quartinia</i> sp. D
	Megachilidae	<i>Heriades</i> sp. J <i>Pseudoheriades primus</i> Peters
Taaiboskraal <i>Leysera tenella</i> DC. Nieuwoudtville	Anthophoridae	<i>Anthophora</i> sp.
	Vespidae: Masarinae	<i>Quartinioides cyllene</i> Richards
	Vespidae: Masarinae	<i>Quartinia artemis</i> Richards <i>Quartinia vagepunctata</i> Schulthess <i>Quartinia</i> sp. D
	Megachilidae	<i>Heriades</i> sp. G

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*Metalasia* R.Br.

*Metalasia muricata* (L.) D.Don.

Nieuwoudtville	Sphecidae	<i>Ammophila ferrugineipes</i> Lepeletier <i>Podalonia canescens</i> (Dahlbom)
	Halictidae	<i>Halictus</i> sp. B <i>Lasioglossum</i> sp. B
	Anthophoridae	<i>Anthophora wartmanni</i> Friese

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*Relbania* L'Herit emend. Bremer

*Relbania pumila* Thunb. (including *Relbania* sp.)

Nieuwoudtville	Vespidae: Masarinae	<i>Quartinia artemis</i> Richards <i>Quartinioides cyllene</i> Richards <i>Quartinia vagepunctata</i> Schulthess <i>Quartinia</i> sp. D

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Tribe 5 : Heliantheae

Flowers usually yellow; mostly American.

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*Verbesina* L.

*Verbesina encelioides* (Cav.) Benth. & Hook.

Fort Brown

Sphecidae

*Ammophila beniniensis*  
(Palisot de Beauvois)

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Tribe 6 : Helenieae

Flowers yellow; warm parts of America, particularly Mexico and the Pacific coast of North America.

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Tribe 7 : Anthemideae

Disc flowers usually yellow; rays white, yellow, or rarely purplish; mostly extra-tropical Old World, particularly the Mediterranean region and South Africa.

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*Athanasia* L.

*Athanasia filiformis* F. f. (including *A. sp.* Grahamstown)

Grahamstown

Tiphiidae

*Anthobosca erythrosoma*  
(Cameron)

*Meria cf. limata* (Smith)

*Meria sp. H*

Pompilidae

*Cyphononyx flavicornis*  
*antennatus* (Smith)

*Hemipepsis tamisieri*  
Guérin-Méneville

Anthophoridae

*Tetraloniella minuta* (Fries)

Halictidae

*Halictus sp. cf. jucundus* Smith

Megachilidae

*Lithurge spiniferus* Cameron  
*Megachile stellarum* Cockerell

*Athanasia trifurcata* (L.) L.

43 km ENE Ceres

Vespidae: Masarinae

*Ceramius toriger* Schulthess  
*Jugurtia turneri* (Schulthess)  
*Quartiniella watersoni*  
 Schulthess

Philanthidae

*Cerceris discrepans discrepans*  
 Brauns  
*Cerceris holconota holconota*  
 Cameron  
*Cerceris latifrons latifrons*  
 Bingham

Halictidae

*Zonalictus* sp. E

Anthophoridae

*Tetraloniella nanula*  
 (Cockerell)

Clanwilliam

Chrysididae

*Allocoelia minor* Mocsáry  
*Chrysis catagrapha* Buysson  
*Pseudospinolia ardoris* Kimsey

Tiphidae

*Meria* sp. H

Vespidae: Masarinae

*Ceramius braunsi* (Schulthess)  
*Masarina mixta* Richards  
*Quartinia persephone* Richards

Pompilidae

*Clavelia ramosa* Smith

Sphecidae

*Schistonyx umbrosus* (Klug)

Nyssonidae

*Podalonia canescens* (Dahlbom)*Bembecinus mutabilis* (Arnold)*Bembix cameronis* Handlirsch*Bembix melanopa* Handlirsch

Philanthidae

*Cerceris languida languida*  
 Cameron

*Philanthus rugosus* Kohl*Philanthus triangulum**diadema* (Fabricius)

Halictidae

*Halictus* sp. cf *jucundus* Smith*Halictus* sp. B*Patellapis* sp. B

Megachilidae

*Capanthidium capicola*  
 (Brauns)

*Heriades* sp. C*Lithurge spiniferus* Cameron

Klein Alexandershoek,  
 Clanwilliam

Vespidae: Masarinae  
 Megachilidae

*Quartinia persephone* Richards  
*Hoplitis* sp. J

Clanwilliam/Klawer	Chrysididae	<i>Allocoelia minor</i> Mocsáry <i>Pseudospinola ardoris</i> Kimsey
	Tiphiidae	<i>Meria</i> sp. H
	Scoliidae	<i>Cathimeris capensis</i> (Saussure)
	Vespidae: Masarinae	<i>Ceramius metanotalis</i> Richards
	Nyssonidae	<i>Bembecinus rhopalocerus</i> (Handlirsch) <i>Bembecinus</i> sp. B <i>Bembix cameronis</i> Handlirsch <i>Bembix capensis</i> Lepeletier <i>Bembix melanopa</i> Handlirsch
	Philanthidae	<i>Cerceris languida languida</i> Cameron <i>Philanthus rugosus</i> Kohl
	Halictidae	<i>Halictus</i> sp. B
	Melittidae	<i>Haplomelitta ogilviei</i> (Cockerell)
	Megachilidae	<i>Capanthidium capicola</i> (Brauns) <i>Hoplitis</i> sp. J
	Anthophoridae	<i>Tetraloniella karooensis</i> (Brauns)
	Halictidae	<i>Lasioglossum</i> sp. C
Theronsberg Pass, Ceres	Halictidae	
<i>Athanasia</i> sp.		
Clanwilliam/ Klawer	Vespidae: Masarinae	<i>Jugurtia braunsiella</i> (Schulthess)
<i>Athanasia</i> spp.		
43 km ENE Ceres	Chrysididae	<i>Chrysis porphyrophana</i> Mocsáry <i>Spintharosoma chrysonota</i> (Dahlbom) <i>Spintharosoma destituta</i> (Dahlbom)
	Tiphiidae	<i>Meria</i> cf. <i>limata</i> (Smith) <i>Meria</i> sp. H
	Scoliidae	<i>Cathimeris capensis</i> (Saussure) <i>Scolia chrysotricha</i> Burmeister <i>Treilis braunsi</i> (Turner)
	Vespidae: Masarinae	<i>Jugurtia turneri</i> (Schulthess)

		<i>Quartiniella watersoni</i> Schulthess
		<i>Quartinioides cyllene</i> Richards
	Pompilidae	<i>Elaphrosyron insidiosus</i> (Smith)
	Crabronidae	<i>Belomicrus</i> sp. C
	Larridae	<i>Palarus latifrons</i> Kohl
	Nyssonidae	<i>Bembix</i> sp.
	Philanthidae	<i>Cerceris discrepans</i> Brauns
		<i>Cerceris holconota holconota</i> Cameron
		<i>Cerceris latifrons latifrons</i> Bingham
		<i>Philanthus melanderi</i> Arnold sp. complex
	Colletidae	<i>Colletes</i> sp. B
		<i>Scapter</i> sp. L
	Halictidae	<i>Halictus</i> sp. A cf. <i>jucundus</i> Smith
		<i>Lasioglossum</i> sp. D
		<i>Nomioides cf. maculiventris</i> (Cameron)
	Megachilidae	<i>Capanthidium capicola</i> (Brauns)
		<i>Heriades</i> sp. A
		<i>Heriades</i> sp. L
	Anthophoridae	<i>Tetraloniella nanula</i> (Cockerell)
60 km ENE Ceres	Colletidae	<i>Scapter</i> sp. K

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*Cotula* L.
*Cotula leptalea* DC.

Nieuwoudtville

Vespidae: Masarinae

*Quartinia vagepunctata*  
Schulthess

Megachilidae

*Heriades* sp. G*Cotula* sp.

Nieuwoudtville

Chrysididae

*Allocoelia glabra* Edney

Vespidae: Masarinae

*Quartinia vagepunctata*  
Schulthess

Crabronidae

*Belomicrus* sp. E



*Cotula* sp.

Anenous

Vespidae: Masarinae

*Quartinia vagepunctata*  
Schulthess*Cotula* sp.

Grahamstown

Megachilidae

*Heriades cf. freygessneri*  
Schletterer*Lasiospermum* Lag.*Lasiospermum bipinnatum* (Thunb.) Druce

Grahamstown

Chrysididae

*Stilbum cyanurum* (Förster)

Vespidae: Eumeninae

*Antepipona scutellaris*

Giordani Soika

*Antepipona sesquicincta*

(Saussure)

*Antepipona* sp.*Antodynerus spoliatus*

(Cameron)

*Eumenes acuminatus* Saussure

Vespidae: Masarinae

*Jugurtia braunsiella*

(Schulthess)

Tiphidae

*Meria* sp. A*Meria* sp. B*Meria cf. basutorum* (Turner)

Scoliidae

*Cathimeris capensis* (Saussure)*Scolia chrysotricha* Burmeister

Crabronidae

*Oxybelus imperialis* Gerstaecker

Sphecidae

*Ammophila beniniensis*

(Palisot de Beauvois)

*Ammophila ferrugineipes*

Lepeletier

*Isodontia simoni* (du Buysson)*Podalonia canescens* (Dahlbom)*Prionyx kirbii*

(Van der Linden)

Nyssonidae

*Bembix cameronis* Handlirsch

Colletidae

*Colletes* sp. A*Scapter* sp. M

Halictidae

*Halictus* sp. cf. *jucundus* Smith*Halictus* spp.

	<i>Lasioglossum</i> sp. E
	<i>Lasioglossum</i> sp. G
	<i>Patellapis</i> sp. C
	<i>Patellapis</i> sp. D
Megachilidae	<i>Heriades</i> cf. <i>spiniscutus</i> (Cameron)
	<i>Heriades</i> sp. A
	<i>Heriades</i> sp. M
	<i>Hoplitis jansei</i> (Brauns)
	<i>Lithurge spiniferus</i> Cameron
	<i>Megachile meadewaldoi</i> (Brauns)
Anthophoridae	<i>Allodapula variegata</i> (Smith)
	<i>Ceratina</i> sp. A
	<i>Ceratina</i> sp. F
	<i>Nomada gigas</i> Friese

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*Pentzia* Thunb.

*Pentzia incana* (Thunb.) Kuntze

Grahamstown	Nyssonidae	<i>Bembecinus oxydorcus</i> (Handlirsch)
	Halictidae	<i>Lipotriches</i> sp. A
Twee Rivieren	Chrysididae	<i>Parnopes fischeri</i> Spinola
	Scoliidae	<i>Trielis stigma</i> (Saussure)
	Nyssonidae	<i>Bembix zinni</i> Gess
	Halictidae	<i>Pseudapis cinerea</i> (Friese)
Prince Albert	Chrysididae	<i>Allocoelia capensis</i> (Smith)
	Anthophoridae	<i>Anthophora praecox</i> Friese
<i>Pentzia suffruticosa</i> (L.) Hutch. ex Merxm.		
Springbok	Vespidae: Masarinae	<i>Ceramius nigripennis</i> Saussure
Wildeperehoek Pass	Vespidae: Masarinae	<i>Quartinia vagepunctata</i> Schulthess
Nieuwoudtville	Tiphiidae	<i>Mesa</i> sp. C
	Vespidae: Masarinae	<i>Jugurtia braunsi</i> (Schulthess)
		<i>Quartinia vagepunctata</i> Schulthess
	Halictidae	<i>Halictus</i> sp. B
	Megachilidae	<i>Heriades</i> sp. A
		<i>Heriades</i> sp. G

43 km ENE Ceres	Chrysididae	<i>Parnopes fischeri</i> Spinola
	Vespididae: Masarinae	<i>Quartiniella watsoni</i> Schulthess
60 km ENE Ceres	Crabronidae	<i>Belomicrus</i> sp. C
	Colletidae	<i>Scapter</i> sp. L <i>Scapter</i> sp. N
<i>Pentzia</i> sp. Clanwilliam	Vespididae: Masarinae	<i>Ceramius braunsi</i> Turner

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### Tribe 8 : Senecioneae

Flowers usually yellow, sometimes white, red, purple, or violet; worldwide.

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#### *Euryops* Cass.

<i>Euryops thunbergii</i> B.Nordenstam		
Nieuwoudtville	Colletidae	<i>Scapter</i> sp. G

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#### *Senecio* L.

##### *Senecio* cf. *arenarius* Thunb.

Clanwilliam/ Graafwater	Vespididae: Masarinae	<i>Celonites bergenwabliae</i> Gess
	Anthophoridae	<i>Sphécodopsis</i> sp.

##### *Senecio burchellii* DC.

43 km ENE Ceres	Vespididae: Masarinae	<i>Jugurtia braunsiella</i> (Schulthess)
	Halictidae	<i>Lasioglossum</i> sp. D
	Megachilidae	<i>Capanthidium capicola</i> (Brauns)

##### *Senecio linifolius* L.

Grahamstown	Halictidae	<i>Halictus</i> spp.
	Megachilidae	<i>Lithurge spiniferus</i> Cameron
	Anthophoridae	<i>Amegilla spilostoma</i> (Cameron)
		<i>Anthophora labrosa</i> Friese
		<i>Anthophora rufolanata</i> Dours
		<i>Anthophora vestita</i> Smith

		<i>Anthophora wartmanni</i> Friese
		<i>Thyreus albomaculatus</i> (De Geer)
<i>Senecio</i> prob. <i>nivea</i> Less		
Nieuwoudtville	Vespidae: Masarinae	<i>Jugurtia polita</i> Richards
		<i>Quartinia</i> sp. D
		<i>Quartinoides cyllene</i> Richards
	Halictidae	<i>Halictus</i> sp. cf. <i>jucundus</i> Smith
	Megachilidae	<i>Heriades</i> sp. A
		<i>Heriades</i> sp. F
		<i>Heriades</i> sp. G
<i>Senecio pterophorus</i> DC.		
Grahamstown	Vespidae: Masarinae	<i>Ceramius lichtensteinii</i> (Klug) (exceptional)
	Tiphiidae	<i>Meria</i> sp. H
	Colletidae	<i>Colletes</i> sp. A
	Halictidae	<i>Halictus</i> sp. A cf. <i>jucundus</i> Smith
		<i>Halictus</i> sp. B
		<i>Zonalictus</i> sp. A
	Megachilidae	<i>Coelioxys penetratrix</i> Smith
		<i>Creightoniella dorsata</i> (Smith)
		<i>Lithurge spiniferus</i> Cameron
		<i>Megachile stellarum</i> Cockerell
	Anthophoridae	<i>Ceratina</i> sp. F
<i>Senecio rosmarinifolius</i> L.f.		
Oudtshoorn	Chrysididae	<i>Allocoelia bidens</i> Edney
		<i>Allocoelia capensis</i> (Smith)
		<i>Chrysis oxygona</i> Mocsáry
		<i>Chrysis splendens</i> Dahlbom
		<i>Parnopes fischeri</i> Spinola
		<i>Spinantharina</i> sp. nr. <i>bispinosa</i> (Mocsáry)
		<i>Spintharosoma chrysonota</i> (Dahlbom)
	Tiphiidae	<i>Meria</i> sp. H
	Scoliidae	<i>Scolia chrysotricha</i> Burmeister
		<i>Scolia fulvofimbriata</i> Burmeister
	Vespidae: Masarinae	<i>Celonites promontorii</i> Brauns
		<i>Ceramius jacoti</i> Richards

		<i>Jugurtia braunsiella</i> (Schulthess)
	Sphecidae	<i>Podalonia canescens</i> (Dahlbom)
	Philanthidae	<i>Cerceris latifrons latifrons</i> Bingham
	Colletidae	<i>Colletes</i> sp. B <i>Scapter</i> sp. L
	Halictidae	<i>Halictus</i> sp. cf. <i>jucundus</i> Smith <i>Halictus</i> sp. B
	Megachilidae	<i>Capanthidium capicola</i> (Brauns) <i>Lithurge spiniferus</i> Cameron <i>Heriades</i> sp. A
	Anthophoridae	<i>Amegilla niveata</i> (Fries) <i>Tetraloniella minuta</i> (Fries) <i>Thyreus calceatus</i> (Vachal) <i>Xylocopa scioensis</i> Gribodo
43 km ENE Ceres	Vespidae: Masarinae	<i>Jugurtia braunsiella</i> (Schulthess) <i>Jugurtia turneri</i> (Schulthess) <i>Podalonia canescens</i> (Dahlbom)
	Sphecidae	<i>Lasioglossum</i> sp. D
	Halictidae	<i>Capanthidium capicola</i> (Brauns)
	Megachilidae	
<i>Senecio</i> sp. Citrusdal	Philanthidae	<i>Cerceris languida languida</i> Cameron
	Colletidae	<i>Scapter</i> sp. H
	Melittidae	<i>Haplomelitta ogilviei</i> (Cockerell)
<i>Senecio</i> sp. Cradock	Vespidae: Masarinae	<i>Jugurtia polita</i> Richards
<i>Senecio</i> sp. Grahamstown	Chrysididae	<i>Chrysis alternans</i> Dahlbom <i>Chrysis catagrapha</i> Buysson <i>Chrysis mionii</i> Guérin- Méneville <i>Chrysis wahlbergi</i> Dahlbom <i>Hedychrum coelestinum</i> Spinola



	Tiphiidae	<i>Meria rufifrons</i> (Fabricius) <i>Meria</i> sp. H
	Vespidae: Eumeninae	<i>Antepipona scutellaris</i> Giordani Soika <i>Delta caffer</i> (L.) <i>Euodynerus</i> sp. <i>Raphiglossa natalensis</i> Smith <i>Raphiglossa flavo-ornata</i> Cameron <i>Zetheumenidion femoratus</i> (Schulthess) <i>Zethus</i> sp.
	Pompilidae	<i>Cyphononyx flavicornis</i> <i>antennatus</i> (Smith) <i>Psammoderes mimicus</i> Haupt
	Sphécidae	<i>Isodontia simoni</i> (du Buysson) <i>Podalonia canescens</i> (Dahlbom)
	Halictidae	<i>Lipotriches</i> sp. A <i>Pachynomia glabriventris</i> (Friese)
	Megachilidae	<i>Heriades</i> cf. <i>freygessneri</i> Schletterer <i>Hoplitis similis</i> (Friese) <i>Lithurge spiniferus</i> Cameron <i>Megachile meadewaldoi</i> (Brauns) <i>Megachile semiflava</i> Cockerell <i>Megachile stellarum</i> Cockerell <i>Pachyanthidium benguelense</i> (Vachal)
	Anthophoridae	<i>Tetraloniella junodi</i> (Friese) <i>Ceratina</i> sp. C <i>Ceratina</i> sp. F
<i>Senecio</i> sp. Nieuwoudtville	Vespidae: Eumeninae	<i>Raphiglossa natalensis</i> Smith
	Vespidae: Masarinae	<i>Jugurtia braunsi</i> (Schulthess) <i>Quartinia persephone</i> Richards <i>Quartinia vagepunctata</i> Schulthess
<i>Senecio</i> sp. Prince Albert	Chrysididae	<i>Parnopes fischeri</i> Spinola

*Senecio* sp.

Springbok

Vespidae: Masarinae

*Jugurtia braunsi* (Schulthess)

## Tribe 9 : Calenduleae

Flowers often yellow, sometimes white, blue, or pink; Old World, particularly the Mediterranean region and South Africa.

*Osteospermum* L.*Osteospermum oppositifolia* (Ait.) T.Norl. (including *O. cf. oppositifolia*)

Nieuwoudtville

Tiphidae

*Mesa* sp. C

Vespidae: Masarinae

*Jugurtia polita* Richards*Quartinia vagepunctata*

Schulthess

Megachilidae

*Heriades* sp. F*Pseudoheriades primus* Peters

## Tribe 10 : Arctoteae

Flowers yellow or purple, occasionally white; Old World, chiefly South Africa.

*Arctotheca* Wendl.*Arctotheca calendula* (L.) Levyns

Springbok

Vespidae: Masarinae

*Ceramius nigripennis* Saussure*Jugurtia braunsi* (Schulthess)*Quartinioides* sp. I

Clanwilliam

Vespidae: Masarinae

*Ceramius braunsi* Turner

Clanwilliam/

Vespidae: Masarinae

*Ceramius braunsi* Turner

Graafwater

Colletidae

*Scapter* sp. E*Scapter* sp. F

Megachilidae

*Hoplitis* sp. B

Anthophoridae

*Tetraloniella junodi* (Fries)

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*Arctotis* L.*Arctotis laevis* Thunb.

Clanwilliam

Vespididae: Masarinae  
Anthophoridae*Ceramius braunsi* Turner  
*Anthophora wartmanni* Friese

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*Berkheya* Ehrh.*Berkheya canescens* DC.

Springbok

Vespididae: Masarinae  
Fideliidae*Ceramius rex* Saussure  
*Fidelia cf. braunsiana* Friese

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*Berkheya carlinifolia* (DC.) Roessler

Ceres

Vespididae: Masarinae  
Megachilidae  
Anthophoridae*Ceramius caffer* Saussure  
*Coelioxys lativentris* Friese  
*Amegilla niveata* (Friese)  
*Anthophora praecox* Friese

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*Berkheya fruticosa* (L.) Ehrh.

Springbok

Vespididae: Masarinae  
Vespididae: Eumeninae*Ceramius nigripennis* Saussure  
*Raphiglossa flavo-ornata*  
Cameron

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Nieuwoudtville

Vespididae: Masarinae

*Celonites promontorii* Brauns  
*Ceramius toriger* Schulthess  
*Quartinoides tarsata* Richards  
*Ammophila ferrugineipes*  
Lepeletier  
*Fidelia braunsiana* Friese  
*Heriades* sp. E  
*Hoplitis* sp. B  
*Tuberanthidium tuberculiferum*  
(Brauns)  
*Heriades* sp. C

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*Berkheya heterophylla* (Thunb.) O.Hoffm.

Grahamstown

Vespididae: Eumeninae

*Allepipona erythrospila*  
(Cameron)

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Pompilidae

*Raphiglossa natalensis* Smith

Crabronidae

*Priocnemis braunsi* Arnold*Dasyproctus bipunctatus*  
*bipunctatus* Lepeletier

Nyssonidae

*Dasyproctus simillimus* (Smith)*Bembix sibilans* Handlirsch

	Halictidae	<i>Halictus</i> sp. cf. <i>jucundus</i> Smith
		<i>Halictus</i> sp. B
	Megachilidae	<i>Chalicodoma sinuata</i> (Friese)
		<i>Creightoniella discolor</i> (Smith)
		<i>Hoplitis similis</i> (Friese)
		<i>Hoplitis jansei</i> (Brauns)
		<i>Hoplitis</i> sp. A
		<i>Megachile stellarum</i> Cockerell
		<i>Serapista denticulata</i> (Smith)
	Anthophoridae	<i>Allodape rufogastra</i> Lep. & Serv. and/or <i>exoloma</i> Strand
		<i>Allodape quadrilineata</i> (Cameron)
		<i>Allodapula variegata</i> (Smith)
		<i>Amegilla atrocincta</i> (Lepeletier)
		<i>Anthophora labrosa</i> Friese
		<i>Anthophora praecox</i> Friese
		<i>Anthophora rufolanata</i> Dours
		<i>Anthophora wartmanni</i> Friese
		<i>Anthophora vestita</i> Smith
		<i>Ceratina</i> sp. C
		<i>Ceratina</i> sp. F
		<i>Ceratina</i> sp. I
		<i>Tetraloniella karoensis</i> (Brauns)
		<i>Thyreus albomaculatus</i> (De Geer)
		<i>Thyreus caffra</i> (Lepeletier)
<i>Berkheya</i> cf. <i>spinosa</i> (L.f.) Druce		
Prince Albert	Vespidae: Masarinae	<i>Celonites promontorii</i> Brauns
		<i>Celonites wheeleri</i> Brauns
		<i>Quartinioides</i> sp. G
<i>Berkheya</i> sp.		
Bot River	Vespidae: Masarinae	<i>Ceramius caffer</i> Saussure
<i>Berkheya</i> sp.		
Clanwilliam	Anthophoridae	<i>Anthophora labrosa</i> Friese
		<i>Anthophora praecox</i> Friese

<i>Berkheya</i> sp. Grahamstown	Anthophoridae	<i>Allodape</i> sp. <i>Xylocopa caffra</i> (L.) <i>Xylocopa scioensis</i> Gribodo
<i>Berkheya</i> sp. Oudtshoorn	Vespidae: Masarinae	<i>Celonites capensis</i> Brauns
<i>Berkheya</i> sp. Riebeek East	Vespidae: Eumeninae Vespidae: Masarinae Halictidae  Megachilidae  Anthophoridae	<i>Raphiglossa natalensis</i> Smith <i>Celonites capensis</i> Brauns <i>Halictus</i> sp. A cf. <i>jucundus</i> Smith <i>Immanthidium junodi</i> (Fries) <i>Megachile stellarum</i> Cockerell <i>Anthophora labrosa</i> Fries <i>Anthophora praecox</i> Fries <i>Anthophora vestita</i> Smith
<i>Berkheya</i> sp. Springbok	Vespidae: Masarinae Anthophoridae	<i>Ceramius nigripennis</i> Saussure <i>Xylocopa sicheli</i> Vachal
<i>Berkheya</i> sp. Williston	Vespidae: Masarinae Anthophoridae	<i>Quartinioides tarsata</i> Richards <i>Tetraloniella karoensis</i> (Brauns)

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*Hirpicium* Cass.

<i>Hirpicium alienatus</i> (Thunb.) Druce Springbok	Vespidae: Masarinae	<i>Ceramius nigripennis</i> Saussure
<i>Hirpicium</i> sp. Springbok	Vespidae: Masarinae	<i>Ceramius nigripennis</i> Saussure

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*Gazania* Gaertn.

<i>Gazania</i> sp. Williston	Vespidae: Masarinae	<i>Quartinioides propinqua</i> (Schulthess) <i>Quartinioides tarsata</i> Richards <i>Quartinioides</i> sp. Z
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Tribe 11 : Cardueae

Flowers blue, purple or reddish, white, or sometimes yellow; mostly Eurasian, particularly the Mediterranean region and the Near East.

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*Cirsium* Mill. emend. Scop.

*C. vulgare*

Grahamstown

Vespidae: Eumeninae

Sphecidae

Anthophoridae

*Raphiglossa natalensis* Smith

*Podalonia canescens* (Dahlbom)

*Anthophora vestita* Smith

*Ceratina* sp. C

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Tribe 12 : Mutiseae

Flowers often purple or red; mostly southern hemisphere, particularly in the Andes.

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Tribe 13 : Lactuceae

Flowers yellow, occasionally blue, purple or white; mostly northern hemisphere.

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PAPILIONACEAE (Fabaceae)

Only members of the Cape Group of the tribe Crotalariaeae are listed, as it is only papilionates from this group which are recorded as being visited by masarines.

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*Aspalathus* L.

*Aspalathus divaricata* Thunberg

Gydo Pass, Ceres

Vespidae: Masarinae

Megachilidae

*Masarina familiaris* Richards

*Masarina* sp. A

*Afranthidium reicherti*

(Brauns)

		<i>Brachichilidium braunsi</i> (Fries)
		<i>Spinanichilidium volkmanni</i> (Fries)
	Anthophoridae	<i>Alloea friesei</i> Strand
		<i>Ceratina</i> sp. J
<i>Aspalathus linearis</i> (Burm. f.) Dahlgren		
Clanwilliam	Vespidae: Masarinae	<i>Ceramius dygatus</i> Richards
		<i>Masarina familiaris</i> Richards
	Philanthidae	<i>Cenosis longula</i> Cameron
		<i>Philanthus triangulum</i> (Fabricius)
	Megachilidae	<i>Brachichilidium braunsi</i> (Fries)
		<i>Chalcidodoma karooensis</i> Brauns
		<i>Chalcidodoma sinuata</i> (Fries)
		<i>Immanichilidium imoidis</i> (Fries)
		<i>Scrapista rufipes</i> Fries
		<i>Spinanichilidium volkmanni</i> (Fries)
	Anthophoridae	<i>Xylocopa ruficornis</i> Lepelletier
Clanwilliam/ Graafwater	Tiphiidae	<i>Mesa</i> sp. A
	Vespidae: Eumeninae	<i>Delta caffer</i> (L.)
	Vespidae: Masarinae	<i>Masarina familiaris</i> Richards
	Megachilidae	<i>Chalcidodoma schultzei</i> (Fries)
		<i>Scrapista rufipes</i> Fries
	Anthophoridae	<i>Xylocopa caffer</i> (L.)
		<i>Xylocopa ruficornis</i> Lepelletier
Nieuwoudtville	Vespidae: Masarinae	<i>Masarina familiaris</i> Richards
	Megachilidae	<i>Chalcidodoma karooensis</i> Brauns
		<i>Chalcidodoma murina</i> Fries
		<i>Megachile</i> sp. C
		<i>Spinanichilidium trachysiforme</i> (Fries)
		<i>Spinanichilidium volkmanni</i> (Fries)
<i>Aspalathus pulicifolia</i> Dahlgren		
Clanwilliam	Vespidae: Masarinae	<i>Ceramius dygatus</i> Richards
		<i>Ceramius mitcheneri</i> Gess
		<i>Ceramius richardsi</i> Gess
		<i>Masarina familiaris</i> Richards

	Nyssonidae	<i>Bembix cameronis</i> Handlirsch
	Megachilidae	<i>Chalicodoma fulva</i> (Smith)
		<i>Chalicodoma karoensis</i> Brauns
		<i>Chalicodoma murina</i> Friese
		<i>Chalicodoma reicherti</i> Brauns
		<i>Chalicodoma sinuata</i> (Friese)
<i>Aspalathus spinescens</i> Thunberg		
Clanwilliam	Chrysididae	<i>Elampus guillarmodi</i> Kimsey
	Tiphiidae	<i>Mesa</i> sp. A
		<i>Mesa</i> sp. C
	Scoliidae	<i>Cathimeris capensis</i> (Saussure)
	Vespidae: Eumeninae	<i>Delta caffer</i> (L.)
		<i>Delta emarginatum</i> (L.)
	Vespidae: Masarinae	<i>Ceramius braunsi</i> Turner
		(atypical)
		<i>Ceramius clypeatus</i> Richards
		<i>Ceramius micheneri</i> Gess
		<i>Masarina familiaris</i> Richards
		<i>Masarina mixta</i> Richards
		(atypical)
	Sphecidae	<i>Ammophila bonaespei</i>
		Lepeletier
	Philanthidae	<i>Philanthus capensis</i> Dahlbom
	Megachilidae	<i>Carinanthidium cariniventre</i>
		(Friese)
		<i>Chalicodoma aridissima</i>
		Cockerell
		<i>Chalicodoma fulva</i> (Smith)
		<i>Chalicodoma karoensis</i> Brauns
		<i>Chalicodoma murina</i> Friese
		<i>Hoplitis</i> sp. C
		<i>Oranthidium</i> sp.
		<i>Spinanthidium neli</i> (Brauns)
		<i>Spinanthidium trachusiforme</i>
		(Friese)
		<i>Spinanthidium volkmanni</i>
		(Friese)
	Anthophoridae	<i>Xylocopa rufitarsis</i> Lepeletier
Clanwilliam/ Graafwater	Scoliidae	<i>Cathimeris capensis</i> (Saussure)
	Vespidae: Eumeninae	<i>Delta caffer</i> (L.)

	Vespididae: Masarinae	<i>Ceramius chypeatus</i> Richards <i>Masarina hyalinipennis</i> Richards <i>Masarina familiaris</i> Richards
	Sphecidae	<i>Podalonia canescens</i> (Dahlbom)
	Philanthidae	<i>Philanthus capensis</i> Dahlbom
	Megachilidae	<i>Carinanthidium cariniceentre</i> (Friese) <i>Megachile</i> sp. B <i>Spinanthidium neli</i> (Brauns) <i>Spinanthidium volkmanni</i> (Friese)
	Anthophoridae	<i>Ceratina</i> sp. F <sup>*</sup> <i>Ceratina</i> sp. H <i>Xylocopa lugubris</i> Lepeletier <i>Xylocopa rufitarsis</i> Lepeletier
Clanwilliam/ Citrusdal	Vespididae: Eumeninae	<i>Delta caffer</i> (L.)
	Vespididae: Masarinae	<i>Ceramius chypeatus</i> Richards <i>Masarina familiaris</i> Richards
	Philanthidae	<i>Philanthus capensis</i> Dahlbom
	Megachilidae	<i>Chalicodoma aridissima</i> Cockerell <i>Chalicodoma fulva</i> (Smith) <i>Chalicodoma karooensis</i> Brauns <i>Chalicodoma murina</i> Friese <i>Megachile</i> sp. B
Citrusdal	Anthophoridae	<i>Xylocopa capitata</i> Smith
	Vespididae: Masarinae	<i>Ceramius chypeatus</i> Richards
	Megachilidae	<i>Braanthidium braunsi</i> Pasteels <i>Spinanthidium volkmanni</i> (Friese)
Citrusdal/ Paleisheuwel	Anthophoridae	<i>Ceratina</i> sp. H
	Vespididae: Eumeninae	<i>Delta caffer</i> (L.)
	Vespididae: Masarinae	<i>Ceramius chypeatus</i> Richards <i>Masarina familiaris</i> Richards
	Megachilidae	<i>Spinanthidium neli</i> (Brauns) <i>Spinanthidium trachusiforme</i> (Friese)

Klein Alexandershoek, Clanwilliam	Vespidae: Eumeninae	<i>Spinanthidium volkmanni</i> (Friese)
		<i>Xylocopa rufitarsis</i> Lapeletier
	Vespidae: Masarinae	<i>Raphiglossa flavo-ornata</i> Cameron
		<i>Ceramius clypeatus</i> Richards
Wuppertal <i>Aspalathus subtingens</i> Eckl. & Zeyh. Grahamstown	Megachilidae	<i>Masarina familiaris</i> Richards
		<i>Spinanthidium volkmanni</i> (Friese)
	Anthophoridae	<i>Xylocopa caffra</i> (L.)
	Megachilidae	<i>Chalicodoma karoensis</i> Brauns
	Vespidae: Eumeninae	<i>Anteipipona sesquicincta</i> (Saussure)
		<i>Delta hottentottum</i> (Saussure)
		<i>Leuconomia</i> sp. A
		<i>Leuconomia</i> sp. C
	Megachilidae	<i>Coelioxys penetratrix</i> Smith
		<i>Megachile gratiosa</i> Gerstaecker
		<i>Megachile semiflava</i> Cockerell
		<i>Megachile spinarum</i> Cockerell
	Anthophoridae	<i>Megachile unguolata</i> Smith
		<i>Allodape rufogastra/exoloma</i>
		<i>Allodapula variegata</i> (Smith)
		<i>Halterapis nigrinervis</i> (Cameron)
<i>Aspalathus vulnerans</i> Thunberg Paleisheuvel	Vespidae: Masarinae	<i>Xylocopa sicheli</i> Vachal
		<i>Masarina familiaris</i> Richards

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### *Lebeckia* Thunberg

<i>Lebeckia sericea</i> Thunberg Springbok	Vespidae: Masarinae	<i>Masarina familiaris</i> Richards
		<i>Masarina hyalinipennis</i> Richards
		<i>Quartinia vagepunctata</i> Schulthess
	Megachilidae	<i>Chalicodoma bullata</i> (Friese) <i>Chalicodoma fulva</i> (Smith)



		<i>Chalicodoma karoensis</i> Brauns
		<i>Chalicodoma murina</i> Friese
		<i>Megachile apiformis</i> Smith
		<i>Serapista rufipes</i> Friese
		<i>Spinanthidium volkmanni</i> (Friese)
Kamieskroon	Vespidae: Masarinae	<i>Masarina hyalinipennis</i> Richards
	Megachilidae	<i>Chalicodoma karoensis</i> Brauns
		<i>Chalicodoma murina</i> Friese
		<i>Spinanthidium volkmanni</i> (Friese)
<i>Lebeckia spinescens</i> Thunberg		
Springbok	Vespidae: Masarinae	<i>Masarina hyalinipennis</i> Richards
	Megachilidae	<i>Chalicodoma karoensis</i> Brauns
		<i>Spinanthidium volkmanni</i> (Friese)

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*Wiborgia* Thunberg

*Wiborgia monoptera* E. Mey.

Springbok	Vespidae: Eumeninae	<i>Zethus yarrowi</i> Giordani Soika
	Megachilidae	<i>Chalicodoma fulva</i> (Smith)
		<i>Spinanthidium trachusiforme</i> (Friese)
		<i>Spinanthidium volkmanni</i> (Friese)
Kamieskroon	Vespidae: Masarinae	<i>Masarina hyalinipennis</i> Richards
	Megachilidae	<i>Chalicodoma karoensis</i> Brauns
		<i>Chalicodoma murina</i> Friese
		<i>Spinanthidium volkmanni</i> (Friese)
<i>Wiborgia</i> sp.		
43 km ENE Ceres	Vespidae: Eumeninae	<i>Delta caffer</i> (L.)
		<i>Delta emarginatum</i> (L.)
		<i>Delta hottentottum</i> (Saussure)
	Colletidae	<i>Colletes</i> sp. B

	Megachilidae	<i>Chalicodoma laminata</i> (Fries)
		<i>Chalicodoma niveofasciata</i> Fries
		<i>Chalicodoma sinuata</i> (Fries)
		<i>Megachile</i> sp. A
	Anthophoridae	<i>Epeolus amabilis</i> Gerstaecker
		<i>Xylocopa scioensis</i> Gribodo
Klein Alexandershoek, Clanwilliam	Melittidae	<i>Melitta capicola</i> Fries

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*Rafnia* Thunberg

<i>Rafnia amplexicaulus</i> Thunberg		
Clanwilliam	Anthophoridae	<i>Xylocopa caffra</i> (L.)
Clanwilliam/ Graafwater	Megachilidae	<i>Chalicodoma cincta</i> (Fabricius)
Klein Alexandershoek, Clanwilliam	Vespidae: Eumeninae	<i>Synagris maxillosa</i> Saussure
	Megachilidae	<i>Chalicodoma cincta</i> (Fabricius)
	Anthophoridae	<i>Xylocopa caffra</i> (L.)
		<i>Xylocopa capitata</i> Smith
Piekenierskloof/ Paleisheuwel	Megachilidae	<i>Chalicodoma cincta</i> (Fabricius)

## CAMPANULACEAE

### Campanuloideae

#### *Wahlenbergia* Schrad. ex Roth

##### *Wahlenbergia annularis* A. DC.

Citrusdal	Halictidae	<i>Halictus (Seladonia)</i> sp. B
	Melittidae	<i>Capicola</i> sp. A
		<i>Capicola</i> sp. C
		<i>Haplomelitta ogilviei</i> (Cockerell)
	Anthophoridae	<i>Ceratina</i> sp. H
Clanwilliam	Vespidae: Masarinae	<i>Masarina mixta</i> Richards
	Melittidae	<i>Capicola</i> sp. A
		<i>Capicola</i> sp. C

Clanwilliam/ Graafwater	Melittidae	<i>Capicola</i> sp. A
		<i>Capicola</i> sp. C
Springbok	Melittidae	<i>Capicola</i> sp. A
		<i>Capicola</i> sp. D
<i>Wahlenbergia cf. constricta</i> V. Brehmer		
Klein Alexandershoek, Clanwilliam	Vespidae: Masarinae	<i>Celonites bergenwahliae</i> Gess
		<i>Quartinia parcepuncta</i> Richards
	Anthophoridae	<i>Ceratina</i> sp. K
<i>Wahlenbergia ecklonii</i> Buek		
Ceres	Vespidae: Masarinae	<i>Celonites capensis</i> Buek
		<i>Quartinia parcepunctata</i> Richards
		<i>Quartinioides</i> sp. U
		<i>Quartinioides</i> sp. H
	Halictidae	<i>Halictus (Seladonia)</i> sp. B
		<i>Lasioglossum</i> sp. H
		<i>Nomioides cf. maculiventris</i> (Cameron)
<i>Wahlenbergia macra</i> Schltr. & V. Brehm.		
Grahamstown	Vespidae: Eumeninae	<i>Parachilus capensis</i> (Saussure)
	Colletidae	<i>Colletes</i> sp. A
	Anthophoridae	<i>Ceratina</i> sp. F
<i>Wahlenbergia paniculata</i> (Thunb.) A. DC.		
Clanwilliam	Tiphiidae	<i>Mesa</i> sp. A
	Vespidae: Masarinae	<i>Ceramius socius</i> Turner
		<i>Celonites wahlenbergiae</i> Gess
		<i>Masarina mixta</i> Richards
		<i>Quartinia parcepunctata</i> Richards
		<i>Quartinia persephone</i> Richards
		<i>Quartinioides</i> sp. N
		<i>Quartinioides</i> sp. S
	Megachilidae	<i>Hoplitis</i> sp. C
	Anthophoridae	<i>Ceratina</i> sp. K
<i>Wahlenbergia pilosa</i> Buek		
Springbok	Vespidae: Masarinae	<i>Quartinia</i> sp. E
		<i>Quartinia</i> sp. G
		<i>Quartinioides</i> sp. M

	Sphecidae	<i>Jugurtia braunsi</i> (Schulthess)
		<i>Ammophila punctaticeps</i> (Arnold)
	Melittidae	<i>Haplomelitta ogilviei</i> (Cockerell)
	Megachilidae	<i>Hoplitis</i> sp. C
<i>Wahlenbergia prostrata</i> A. DC.		
Anenous	Vespidae: Masarinae	<i>Quartinoides</i> sp. M
	Crabronidae	<i>Belomicroides</i> sp.
	Melittidae	<i>Capicola</i> sp. E
		<i>Melitta capicola</i> Friese
<i>Wahlenbergia psammophila</i> Schltr.		
Clanwilliam/ Graafwater	Vespidae: Masarinae	<i>Celonites wahlenbergiae</i> Gess
		<i>Celonites latitarsis</i> Gess
		<i>Celonites bergenwabhiae</i> Gess
		<i>Masarina mixta</i> Richards
	Melittidae	<i>Capicola</i> sp. C
<i>Wahlenbergia</i> sp. N		
Nieuwoudtville	Vespidae: Masarinae	<i>Masarina mixta</i> Richards
		<i>Quartinoides</i> sp. N
	Sphecidae	<i>Podalonia canescens</i> (Dahlbom)
	Halictidae	<i>Halictus</i> ( <i>Seladonia</i> ) sp. B
	Melittidae	<i>Capicola</i> sp. C
	Anthophoridae	<i>Anthophora wartmanni</i> Friese
		<i>Ceratina</i> sp. H
		<i>Ceratina</i> sp. J
		<i>Ceratina</i> sp. K
<hr/> <i>Microcodon</i> A. DC.		
<i>Microcodon sparsiflora</i> A. DC.		
Clanwilliam	Vespidae: Masarinae	<i>Celonites wahlenbergiae</i> Gess
		<i>Quartinia parcepunctata</i> Richards
		<i>Quartinia persephone</i> Richards

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 Lobelioideae
 

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*Lobelia* L.

*Lobelia linearis* Thunberg

Nieuwoudtville

Vespidae: Masarinae

Anthophoridae

*Celonites* sp. E*Ceratina* sp. H

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*Monopsis* Salisb.

*Monopsis debilis* (L. f.) Presl.

Springbok

Melittidae

*Haplomelitta ogilviei*  
(Cockerell)

Clanwilliam/

Graafwater

Melittidae

*Haplomelitta ogilviei*  
(Cockerell)

Citrusdal

Melittidae

*Haplomelitta ogilviei*  
(Cockerell)

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 SCROPHULARIACEAE
 

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*Aptosimum* Burch.

*Aptosimum procumbens* (Lehm.) Steud.

Grahamstown

Tiphiidae

*Meria* sp. H

Vespidae: Masarinae

*Celonites clypeatus* Brauns

Halictidae

*Quartinioides tarsata* Richards
*Pachynomia glabriventris*  
(Fries)

Megachilidae

*Megachile gratiosa* Gerstaecker

Anthophoridae

*Ceratina* sp. F
*Aptosimum lineare* Marloth & Engl.

Springbok

Vespidae: Masarinae

*Celonites peliostomi* Gess
*Aptosimum spinescens* (Thunb.) Weber

Springbok

Vespidae: Masarinae

*Celonites andrei* Brauns*Celonites peliostomi* Gess*Celonites andrei* Brauns*Celonites clypeatus* Brauns

Halictidae

*Nomioides* sp. A

*Aptosimum* sp.

Kakamas

Andrenidae

*Meliturgula* sp. B

Twee Rivieren

Vespididae: Masarinae

*Celonites clypeatus* Brauns

Andrenidae

*Meliturgula* sp. B*Peliostomum* Benth.*Peliostomum leucorrhizum* E. Mey. ex Benth.

Kakamas

Vespididae: Masarinae

*Quartinioides tarsata* Richards

Twee Rivieren

Vespididae: Masarinae

*Quartinioides tarsata* Richards*Quartinioides* sp. V*Quartinioides* sp. W*Quartinioides* sp. X

Williston

Vespididae: Masarinae

*Quartinioides tarsata* Richards*Peliostomum virgatum* E. Mey. ex Benth.

Anenous

Vespididae: Masarinae

*Celonites peliostomi* Gess*Quartinioides tarsata* Richards*Quartinioides* sp. T*Quartinioides* sp. Y

Nieuwoudtville

Vespididae: Masarinae

*Celonites peliostomi* Gess

Springbok

Vespididae: Masarinae

*Celonites andrei* Brauns*Celonites clypeatus* Brauns*Celonites peliostomi* Gess*Phyllopodium* Benth.*Phyllopodium cuneifolium* (L. f.) Benth.

Grahamstown

Vespididae: Masarinae

*Celonites capensis* Brauns

Pompilidae

*Elaphrosyrus insidiosus*

(Smith)

Sphecidae

*Ammophila beniniensis*

(Palisot de Beauvois)

*Ammophila conifera* (Arnold)*Ammophila ferrugineipes*

Lepeletier

*Ammophila insignis litoralis*

(Arnold)

*Podalonia canescens*

(Dahlbom)



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Nyssonidae	<i>Bembecinus haemorrhoidalis</i> (Handlirsch)
	<i>Bembix sibilans</i> Handlirsch
Halictidae	<i>Halictus (Seladonia)</i> sp. B
Anthophoridae	<i>Allodapula variegata</i> (Smith)

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*Polycarena* Benth.

*Polycarena* sp.

Clanwilliam/  
Graafwater

Vespidae: Masarinae  *Celonites bergenwabliae* Gess

*Celonites wahlenbergiae* Gess

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## APPENDIX 3

### *Described species of masarine wasps*

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Within tribes and subtribes the genera and species are arranged in alphabetical order.

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## MASARINAE

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### Gayellini

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#### *Gayella* Spinola, 1851

*araucana* Willink, 1956; Chile

*eumenoides* Spinola, 1851; Argentina, Chile

*sicheliana* Schulthess, 1910

*luispenai* Willink and Ajmat de Toledo, 1979; Argentina, Bolivia

*mutilloides* Saussure, 1855; Argentina, Chile

*mutilloides nigerrima* Giordani Soika, 1956

*patagonica* Willink, 1956; Argentina, Chile

*cerceroides* Giordani Soika, 1958

*reedi* Willink, 1963; Chile

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#### *Paramasaris* Cameron, 1901

*brasiliensis* Giordani Soika, 1974; Brazil

*cupreus* Giordani Soika, 1974; Columbia

*fuscipennis* Cameron, 1901; Guatemala, Panama, USA: New Mexico

*flavolineatus* Cameron, 1904 (*Zethoides*)

*flavolineatus* Cameron, 1905 (*Plesiozethus*)

*flavolineatus* Schulz, 1906 (*Metazethoides*)

*richardsi* (Giordani Soika), 1974 (*Paragayella*); Brazil

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Masarini: Paragiina

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*Ammoparagia* Snelling, 1986

*bua* Snelling, 1986; W. Australia

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*Metaparagia* Meade-Waldo, 1911

*doddi* Meade-Waldo, 1911; Queensland  
*pictifrons* (Smith), 1857 (*Paragia*); W. Australia

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*Paragia* Shuckard, 1837

*australis* Saussure, 1853; New South Wales  
    *ssp. borealis* Richards, 1962; Queensland  
*bicolor* Saussure, 1853; New South Wales  
*calida* Smith, 1865; S. Australia, W. Australia  
*deceptrix* Smith, 1862; New South Wales, Queensland  
*decipiens* Shuckard, 1837; New South Wales, S. Australia, Victoria  
    *ssp. aliciae* Richards, 1962; Northern Territories, Queensland  
*generosa* Richards, 1962; Queensland  
*hirsuta* Meade-Waldo, 1911; Queensland  
*magdalena* Turner, 1908; Queensland  
*mimetica* Richards, 1968; W. Australia  
*monocesta* Snelling, 1986; W. Australia  
*morosa* Smith, 1868; W. Australia  
*nasuta* Smith, 1868; Queensland, W. Australia  
*odyneroides* Smith, 1850; New South Wales, Queensland, S. Australia, Victoria  
    *bidens* Saussure, 1855  
    *praedator* Saussure, 1855  
*oligomera* Snelling, 1986; W. Australia  
*perkinsi* Meade-Waldo, 1911; Queensland  
*propodealis* Richards, 1968; New South Wales  
*schulthessi* Turner, 1936; W. Australia  
*smithii* Saussure, 154; S. Australia, Victoria  
    *tricolor* Smith, 1850 (not female)  
*sobrina* Smith, 1869; W. Australia  
    *excellens* Smith, 1869  
*tricolor* Smith, 1850 (not male); W. Australia  
    *saussurei* Smith, 1857

*venusta* Smith, 1865; W. Australia  
*concinna* Smith, 1865  
*vespiformis* Smith, 1865; W. Australia  
*walkeri* Meade-Waldo, 1910; Northern Territories, Queensland

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### *Riekia* Richards, 1962

*confluens* (Snelling), 1986 (*Paragia*); W. Australia  
*nocatunga* Richards, 1962; New South Wales, Queensland

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### *Rolandia* Richards, 1962

*angulata* (Richards), 1968 (*Riekia*); New South Wales, Queensland  
*borreriae* Snelling, 1986; Northern Territory  
*houstoni* Snelling, 1986; W. Australia  
*maculata* (Meade-Waldo), 1910 (*Paragia*); W. Australia

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## Masarini: Masarina

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### *Celonites* Latreille, 1802

*abbreviatus* (Villers), 1789 (*Vespa*); Albania, Corfu, Cyprus, Dalmatia, S. France, S. Germany, Greece, Italy, Portugal, Switzerland, Morocco  
*apiformis* (Fabricius), 1793 (*Masaris*)  
ssp. *engadinensis* Schulthess, 1923; Switzerland  
ssp. *invitus* Gusenleitner, 1973; Armenia, Turkey  
*afer* Lepeletier, 1841; Algeria, Libya, Morocco, Tunis  
*andrei* Brauns, 1905; Cape Province  
*bergenwahliae* Gess, 1989; Cape Province  
*capensis* Brauns, 1905; Cape Province  
*clarus* Gusenleitner, 1973; Iran  
*clypeatus* Brauns, 1913; Cape Province  
*crenulatus* Morawitz, 1888; USSR: Transcaspia, Turkestan, Turkmenia  
*cyprius* Saussure, 1854; Cyprus  
ssp. *smyrnensis* Richards, 1962; Armenia, Greece, Iran, Israel, Turkey  
*davidi* Gess, 1989; Cape Province

- discretus* Gusenleitner, 1973; Iran  
*fischeri* Spinola, 1838; Algeria, Cyprus, Egypt, Israel, Libya, Saudi Arabia, Tunis  
*foveolatus* Kostylev, 1935; USSR: Transcaspia  
     ssp. *nigrior* Richards, 1962; Israel, Turkey  
*guichardi* Richards, 1962; Libya  
*hamanni* Gusenleitner, 1973; Jordan, Turkey  
*hystrix* Kostylev, 1940; USSR: Tadjikistan  
*humeralis* Richards, 1962; Cape Province  
*jousseaumei* du Buysson, 1906; Algeria, Arabia (Aden, Oman, Yemen, Saudi Arabia, United Arab Emirates, Qatar), French Somaliland, Palestine, Sudan  
     *asrensis* Giordani Soika, 1957  
     ssp. *senegalensis* Richards, 1962; Mali, Senegal  
*kozlovi* Panfilov, 1961; USSR: Kirghizia  
*kozlovi* Kostylev, 1935; USSR: Mongolia  
*laetus* Panfilov, 1968; USSR  
*latitarsis* Gess, 1992; Cape Province  
*longipilis* Gusenleitner, 1973; Iran  
*mayeti* Richards, 1962; France, Spain  
*michaelseni* Schulthess, 1923; Namibia  
*modestus* Kostylev, 1935; USSR: Pamir  
     ssp. *bisinterruptus* Kostylev, 1940; USSR: Tadjikistan  
*mongolicus* Morawitz, 1889; USSR: Mongolia  
*montanus* Mocsáry, 1906; Alai Mts  
*nursei* Dover, 1925; Quetta  
*octoannulatus* Kostylev, 1927; USSR: Turkestan  
     ssp. *bissaricus* Kostylev, 1940; USSR: Tadjikistan  
*osseus* Morawitz, 1888; USSR: Transcaspia, Turkmenistan  
*peliosomi* Gess, 1989; Cape Province  
*persicus* Richards, 1962; South West Iran  
*phlomis* Gusenleitner, 1973; Turkey  
*pictus* Richards, 1962; Senegal  
     ssp. *rufiventris* Gusenleitner, 1992; Iran  
*promontorii* Brauns, 1905; Cape Province  
*purcelli* Brauns, 1905; Cape Province  
*rothschildi* du Buysson, 1906; Iran, ?Kenya  
*rudesculptus* Kostylev, 1935; Armenia  
*rugiceps* Bischoff, 1928; Crete, Cyprus, Greece, Jugoslavia, Turkey  
*semenovi* Kostylev, 1935; Iran  
*spinosus* Gusenleitner, 1966; Turkey  
*tristiculus* Kostylev, 1935; USSR  
     ssp. *karataucicus* Kostylev, 1935; USSR: Kazakhstan

*turneri* Richards, 1962; Cape Province  
*varipennis* Richards, 1962; Libya  
*wahlenbergiae* Gess, 1989; Cape Province  
*wheeleri* Brauns, 1905; Cape Province  
*yemenensis* Giordani Soika, 1957; Saudi Arabia, Yemen  
     ssp. *ethiopicus* Richards, 1962; Ethiopia  
*zavattarii* Giordani Soika, 1944; Ethiopia

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*Ceramiopsis* Zavattari, 1910

*gestroi* Zavattari, 1910; Argentina, Bolivia, Brazil  
     ? *paraguayensis* Bertoni, 1923

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*Ceramius* Latreille, 1810

*beaumonti* (Giordani Soika), 1957 (*Paraceramius*); Algeria, Morocco  
*beyeri* Brauns, 1903; Cape Province  
*bicolor* (Thunberg), 1815 (*Philanthus*); Cape Province  
     *karooensis* Brauns, 1902  
*bischoffi* Richards, 1963; Spain  
*braunsi* Turner, 1935; Cape Province  
*buresschi* Atannasov, 1938; Greece, Turkey  
     *buresschi lycaonius* Blüthgen, 1952  
*caffer* Saussure, 1855; Cape Province  
     *consobrinus* Saussure, 1855  
*capicola* Brauns, 1902; Cape Province, Orange Free State  
*caucasicus* Ed. André, 1884; Iran, Russian Armenia, Turkey  
*cerceriformis* Saussure, 1853; Cape Province  
     *schulthessi* Brauns, 1902  
     *vespiformis* Saussure, 1855  
*clypeatus* Richards, 1962; Cape Province  
*damarinus* Turner, 1935; Namibia  
*fonscolombeii* Latreille, 1810; France, Portugal, Spain  
     ssp. *oraniensis* Lepeletier, 1841; Algeria, Morocco  
     *doursii* Ed. André, 1884  
*hispanicus* Dusmet, 1909; Spain  
*jacoti* Richards, 1962; Cape Province



*lichtensteinii* (Klug), 1810 (*Gnatho*); Cape Province  
*macrocephalus* Saussure, 1854  
*rufomaculatus* Cameron, 1906  
*linearis* Klug, 1824; Cape Province  
*fumipennis* Brauns, 1902  
*lusitanicus* Klug, 1824; Gibraltar, Portugal, Spain  
*maroccanus* (Giordani Soika), 1957 (*Paraceramius*); Morocco  
     ssp. *rubripes* Gusenleitner, 1990; Morocco  
*metanotalis* Richards, 1962; Cape Province  
*micheneri* Gess, 1968; Cape Province  
*montanus* Gusenleitner, 1990; Morocco  
*nigripennis* Saussure, 1854; Cape Province  
     *bessei* Turner, 1935  
*palaestinensis* (Giordani Soika), 1957 (*Paraceramius*); Israel, Turkey  
*peringueyi* Brauns, 1913; Cape Province  
*rex* Saussure, 1855; Cape Province  
*richardsi* Gess, 1965; Cape Province  
*socius* Turner, 1935; Cape Province  
*spiricornis* Saussure, 1854; France, Spain  
*toriger* Schulthess, 1935; Cape Province  
*tuberculifer* Saussure, 1853; France, Portugal, Spain  
*vechti* Richards, 1963; Spain

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### *Jugurtia* Saussure

*alfkeni* (du Buysson), 1904 (*Masaris*); Kalahari  
*algerica* (Schulthess), 1929 (*Masariella* ?); Algeria, Morocco, Tripolitania  
*biskrensis* Bequaert, 1937; Algeria, Morocco  
*braunsi* (Schulthess), 1922 (*Ceramiellus*); Cape Province, Namibia  
*braunsiella* (Schulthess), 1930 (*Masaris*); Cape Province, Namibia  
*calcarata* Richards, 1962; Cape Province  
*confusa* Richards, 1962; Cape Province  
*discrepans* (Brauns), 1913 (*Masaris*); Cape Province  
*dispar* (Dufour), 1851 (*Celonites*); Gibraltar, Portugal, Spain  
*duplicata* Richards, 1962; Cape Province  
*escalerae* Meade-Waldo, 1910; S. W. Iran, Turkey  
*eurycara* Kostylev, 1935; Iran, Turkey, USSR: Armenia  
*irana* Kostylev, 1935; Iran  
*jemenensis* Kostylev, 1935; Algeria, Oman, Palestine, Saudi Arabia, United Arab Emirates, Yemen

*boggarica* Giordani Soika, 1954  
*nadigorum* Bequaert, 1937; Morocco, Tanger  
*oraniensis* (Lepeletier), 1841 (*Celonites*); Algeria, Morocco, Tunisia  
*numida* Saussure, 1854  
*polita* Richards, 1962; Cape Province  
*saussurei* (Brauns), 1905 (*Masaris*); Cape Province  
*simpsoni* Meade-Waldo, 1911; Gambia, ? Haute Volta, N. Nigeria, Senegal  
*testaceopicta* (Schulthess), 1929 (*Masariella* ?)  
*spinolae* (Saussure), 1855 (*Masaris*); Cape Province  
*turneri* (Schulthess), 1929 (*Masariella* ?); Cape Province  
*ssp. eburnea* Turner, 1935; Cape Province  
*zarudnyi* Kostylev, 1935, Iran, USSR: Chorassan

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### *Masarina* Richards, 1962

*familiaris* Richards, 1962; Cape Province  
*hyalinipennis* Richards, 1962; Cape Province  
*mixta* Richards, 1962; Cape Province  
*strucki* Gess, 1988; Cape Province

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### *Masaris* Fabricius, 1793

*aegyptiacus* Meade-Waldo, 1911; Egypt, Israel  
*ssp. arabicus* Giordani Soika, 1957; Saudi Arabia  
*carli* Schulthess, 1922; Iran, USSR: Turkestan  
*saussurei* Carl, 1921  
*smirnovi* Kostylev, 1925  
*gussakovskii* Kostylev, 1935; USSR: Turkestan  
*longicornis* (Kuznetsov), 1923 (*Saryara*); Afghanistan, USSR: Tashkent and Buchara  
*tiashanicus* Panfilov, 1968; USSR: Tyan-Shan  
*vespiformis* Fabricius, 1793; Algeria, Morocco  
*hylaeiformis* (Klug), 1824 (*Ceramius*)  
*romandi* (Saussure), 1853 (*Erynnis*)

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### *Microtrimeria* Bequaert, 1928

*atacama* Fritz, 1968; Chile  
*cockerelli* Bequaert, 1928; Peru

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*Pseudomasaris* Ashmead, 1902

- basirufus* Rohwer, 1912; USA: Arizona, California  
*zonalis basirufus* Rohwer, 1912  
*bariscipus* Bradley, 1922  
*coquillettii* Rohwer, 1911; USA: Arizona, California, Oregon, Utah  
*edwardsii* (Cresson), 1872 (*Masaris*); Mexico: Baja California, USA: Arizona, California, Colorado, Idaho, Nevada, Oregon, Utah, Washington, Wyoming  
*macneilli* Bohart, 1963; USA: California, Utah  
*macswaini* Bohart, 1963; USA: California  
*maculifrons* (Fox), 1894 (*Masaris*); Mexico: Baja California, Sonora, USA: Arizona, California, Nevada, New Mexico  
*albifrons* Rohwer, 1912  
*zonalis neomexianus* Rohwer, 1912  
*rohweri* Bradley, 1922  
*marginalis* (Cresson), 1864 (*Masaris*); Canada: Alberta, B.C., USA: Colorado, Montana, Nevada, New Mexico, Utah, Wyoming  
*micheneri* Bohart, 1963; USA: California  
*occidentalis* (Cresson), 1871 (*Masaris*); USA: Kansas, New Mexico, Texas  
*phaceliae* Rohwer, 1912; USA: New Mexico  
*texanus* (Cresson), 1871 (*Masaris*); USA: Arizona, New Mexico, Texas  
*vespoides* (Cresson), 1863 (*Masaris*); Mexico: Baja California, USA: Arizona, California, Colorado, Idaho, Montana, Nebraska, Nevada, New Mexico, Oregon, S. Dakota, Utah, Washington, Wyoming  
*vespoides robertsoni* Cockerell, 1913  
*wheeleri* Bequaert, 1929; Mexico: Baja California, USA: California  
*zonalis* (Cresson), 1864 (*Masaris*); Canada: B.C., USA: California, Colorado, Idaho, Montana, Nebraska, Nevada, Oregon, Utah, Washington, Wyoming  
*zonalis albopictus* Bohart, 1950

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*Quartinia* Ed. André

- affinis* Richards, 1962; Algeria  
*alcestis* Richards, 1962; Cape Province  
*antennata* Schulthess, 1935; Cape Province  
*araxana* Giordani Soika, 1960; Caucasus  
*artemis* Richards, 1962; Cape Province  
*atra* Schulthess, 1929; Cape Province  
*breyeri* Richards, 1962; ?Transvaal  
*canariensis* Blüthgen, 1958; Canary Islands

- cincta* Benoist, 1929; Morocco  
*chlorotica* (Morawitz), 1888 (*Jugurtia*); USSR: Transcaspia  
*cretica* Gusenleitner, 1994; Greece: Crete  
*dilecta* Ed. André, 1884; Algeria, Morocco, Tunisia  
*eremobia* Richards, 1962; Algeria; Tripolitania  
*funebria* Kostylev, 1935; USSR: Transcaspia  
*goleana* Richards, 1962; Algeria  
*guichardi* Richards, 1969; Canary Islands  
*haemmorrhoea* ?  
     ssp. *frontalis* Blüthgen, 1961; Afganistan  
*halicticeps* Giordani Soika, 1939; Egypt  
*hypatia* Richards, 1962; Cape Province  
*indica* Cameron, 1904; India (Deesa)  
*jocasta* Richards, 1962; Cape Province  
*lesnei* Benoist, 1929; Algeria  
*libanica* Richards, 1964; Cyprus, Lebanon  
*major* Kohl, 1898; Algeria, Morocco  
*media* Schulthess, 1929; Cape Province  
*medusa* Richards, 1962; Namibia  
*mochii* Giordani Soika, 1939; Egypt  
*mongolica* Morawitz, 1889; USSR: S. Mongolia  
*nilotica* Fischer, 1964; Egypt  
*nubiana* Richards, 1962; Egypt, Libya, Saudi Arabia, Sudan, Tunisia  
*ochraceopicta* Schulthess, 1932; Namibia  
*orientalis* Gusenleitner, 1973; Afganistan, Turkey  
*paradoxa* Brauns, 1905; Cape Province  
*parcepunctata* Richards, 1962; Cape Province  
*parvula* Dusmet, 1909; Portugal, Spain  
*perone* Richards, 1962; Cape Province  
*persephone* Richards, 1962; Cape Province  
*pluto* Richards, 1962; Cape Province  
*popovi* Gussakovskii, 1936; USSR  
*proserpina* Richards, 1962; Cape Province  
*punctulata* Schulthess, 1930; Cape Province  
*pusilla* Kostylev, 1935; USSR: Turkmenistan  
*shestakovi* Kostylev, 1935; USSR (Asiatic Russia)  
*soikai* Richards, 1964; Turkey  
*syriaca* Richards, 1964; Lebanon, Syria  
     ssp. *nitens* Gusenleitner, 1973; Iran  
*tenerifina* Richards, 1969; Canary Islands  
*thebaica* du Buysson, 1902; Algeria, Egypt, Morocco, Tripolitania

*tricolorata* Giordani Soika, 1954; Egypt  
*tripolitana* Richards, 1962; Cyrenaica, Egypt, Tripolitania  
 ssp. *sinaitica* Richards, 1964; UAR: Sinai  
*tuareg* Giordani Soika, 1954; Algeria, Egypt  
*uzbeka* Kostylev, 1935; USSR (Asiatic Russia)  
*vagepunctata* Schulthess, 1929; Cape Province

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### *Quartiniella* Schulthess, 1929

*flava* Richards, 1962; Cape Province  
*minuscule* Turner, 1939; Cape Province  
*striata* Richards, 1962; Cape Province  
*turneri* Schulthess, 1932; Namibia  
*waterstoni* Schulthess, 1929; Cape Province

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### *Quartinioides* Richards, 1962

*albopicta* Richards, 1982; Namibia  
*andromeda* Richards, 1962; Cape Province  
*antigone* Richards, 1962; Cape Province  
*arsinoe* Richards, 1962; Cape Province, Namibia  
*basuto* Richards, 1962; Lesotho  
*capensis* (Kohl), 1898 (*Quartinia*); Cape Province  
*scutellimacula* Schulthess, 1929 (*Quartinia*) (in part)  
*ceres* Richards, 1962; Cape Province  
*cressida* Richards, 1962; Cape Province, Namibia  
*cyllene* Richards, 1962; Cape Province  
*cynara* Richards, 1962; Cape Province  
*diana* Richards, 1962; Namibia  
*dryope* Richards, 1962; Cape Province  
*elissa* Richards, 1962; Cape Province  
*eurydice* Richards, 1962; Cape Province  
*galataea* Richards, 1962; Cape Province  
*hecuba* Richards, 1962; Cape Province, ?Natal  
*belena* Richards, 1962; Cape Province  
*belichrysi* Richards, 1962; Lesotho  
*betaira* Richards, 1962; Cape Province  
*interrupta* (Turner), 1939 (*Quartinia*); Cape Province, Namibia  
*ipbigenia* Richards, 1962; Namibia

*laeta* (Schulthess), 1935 (*Quartinia*); Namibia  
*latona* Richards, 1962; Cape Province  
*maerens* (Schulthess), 1935 (*Quartinia*); Cape Province  
*matabele* (Turner), 1939 (*Quartinia*); Zimbabwe  
*metallescens* (Schulthess), 1929 (*Quartinia*); Cape Province, Lesotho  
*metope* Richards, 1962; Namibia  
*minima* (Schulthess), 1932 (*Quartinia*); Namibia  
*multipicta* Richards, 1962; Cape Province  
*niveopicta* (Schulthess), 1930 (*Quartinia*); Cape Province  
*philomela* Richards, 1962; Cape Province  
*phoebe* Richards, 1962; Cape Province  
*poecila* (Schulthess), 1930 (*Quartinia*); Namibia  
*propinqua* (Schulthess), 1932 (*Quartinia*); Cape Province, Namibia  
*senecionis* Richards, 1962; Lesotho, Orange Free State  
*signata* (Schulthess), 1929 (*Quartinia*); Cape Province  
*signatifrons* (Turner), 1932 (*Quartinia*); Cape Province  
*tarsata* Richards, 1962; Cape Province  
*titania* Richards, 1962; Cape Province

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### *Trimeria* Saussure, 1854

*americana* (Saussure), 1853 (*Erynnis*); Brazil  
*bequaerti* Willink, 1951; Argentina, Bolivia  
*buyssoni* Brèthes, 1904; Argentina, Paraguay  
*howardi* Bertoni, 1912; Argentina, Paraguay  
*joergenseni* Schrottky, 1909; Argentina  
*monrosi* Willink, 1959; Argentina  
*neotropica* (Mocsáry), 1906 (*Jugurtia*); Paraguay





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